Temporal Variation in the Diet and Feeding Intensity of Snoek (*Thyrsites atun*) in the Southern Benguela Upwelling System

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Dr. M.H. Griffiths

Dedicated to my parents,

Deanne and Drummond McQueen

…with love, and my eternal gratitude.

Declaration

This dissertation documents the results of original research carried out at Marine and Coastal Management and in the Marine Biology Research Institute, Zoology Department, at the University of Cape Town. It has not been submitted in whole or in part for any other degree or examination at any other university. The data presented were obtained from Marine and Coastal Management, Department of Environmental Affairs. Data from 1994 – 1999 were collected and processed by Dr. M. H. Griffiths and research staff at Marine and Coastal Management. Data from 2000-2002 were collected and processed by myself and research staff. All opinions expressed here, unless otherwise acknowledged, are my own. All assistance received has also been fully acknowledged.

Signed by candidate

Nicola Jane McQueen

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Contents

Abstract

Temporal variation in the diet and feeding intensity of snoek (*Thyrsites atun*), a top predator of commercially exploited pelagic clupeoids, was investigated in the Southern Benguela Upwelling System.

A pilot study investigated the appropriate sample sizes required to produce accurate daily or event-scale diet descriptions in this predator, by means of *a posteori* tests. Using cumulative prey diversity curves, it was estimated that 55 (± 25) stomachs containing food were required to accurately quantify presence and absence data for prey species. In order to describe exact prey proportions, cumulative percentage graphs produced a figure of 75 – 80 (± 25) stomachs containing food per sample. An equation cited by Duffy and Jackson (1986) was used to calculate optimum sample sizes. The results indicated a median number of between 90 – 100 (± 45) stomachs were needed to give an estimate of the proportion of the main prey type that was within 10% of the probable value, however the estimated totals relied heavily on the prey proportions in the diet. The decline in the standard error associated with the main prey proportion with increasing sample size, was demonstrated to reach the 5% level after 88.9 (± 12.7) stomachs examined offshore, and 85.7 (± 20.7) stomachs inshore. Additional techniques for improving general precision in diet estimates were investigated, as well as appropriate methods for statistical analysis of diet samples.

A study of seasonal variation in the prey proportions in the diet of snoek was conducted using data from 1994 – 1997, around the Cape Peninsula. The major prey species consumed by snoek over this period were pilchard (*Sardinops sagax*), followed by anchovy (*Engraulis encrasicolus*). No marked patterns of seasonal variation in availability or relative proportions in the diet occurred in these species. Lesser prey types such as round herring (*Etrumeus whiteheadi*), horse mackerel (*Trachurus trachurus capensis*), mantis shrimps (*Pterygosquilla armata capensis*) and hake *(Merluccius spp.*) showed subtle seasonal variations in the diet, believed to be linked to their spawning and migration patterns through the area sampled. There was no significant statistical seasonal diet similarity (like-seasons, across years) based on prey proportions (ANOSIM: $R = 0.143$; $p = 0.17$), but regional (inshore-offshore) diet differences were significant (ANOSIM: $R = 0.885$; $p = 0.029$). The difference between inshore and offshore diets was characterised by the presence of hake, and the absence of anchovy, in the offshore samples. Positive correlations existed between the relative proportions of pilchard and anchovy in snoek diet and in purse-seine catches made in the area sampled over the period of the study (Pearson: $r = 0.6$). There was, however, a significantly higher degree of selectivity by snoek for anchovy than for pilchard (ttest: $p < 0.001$).

An investigation of the physiology and feeding intensity was undertaken over the aforementioned period. Snoek were found to peak in relative condition and fat content in summer and autumn, during their non-spawning periods, at which time the Gonadosomatic Index (GSI) was at its lowest. Significantly lower levels of fat and condition occurred during spawning months (winter and spring), at which time feeding intensity was significantly higher. This relationship between feeding and spawning was concluded to conform to a 'ramper' pattern, as defined by Link and Burnett (2001). Fat content in females was found to be significantly lower than that in males during spawning periods, despite the fact that female feeding intensity was significantly higher. This indicated that the costs of reproduction might be higher for female fish than for males.

Diurnal feeding periodicity during the day, and 24-hr and week-to-week variation in diet were investigated. It was found that snoek exhibited no clear repeated diel feeding periodicity, and that feeding in the population was essentially continuous throughout the 24-hr cycle. There was evidence that snoek availability to the trawlers in one offshore region was linked to the presence of its preferred prey types (clupeoids) in that area. From the proportions of fish with stomachs containing food and the relative freshness of prey items, it appeared that snoek fed both by night and day. From the diel vertical distribution patterns of its main prey species and the fact that no snoek were caught on the bottom at night, it was concluded that daytime feeding took place in the lower water strata (100 – 250 m) whereas at night they fed on the surface. Week-to-week variation in the diet was extensive. Prey proportions showed no significant similarity from week to week or to the average over the six-week period (ANOSIM: $R = -0.68$, $p = 0$). This dissimilarity serves to demonstrate the importance of regular and frequent sampling in order to accurately quantify relative prey proportions in the diet over an extended period (e.g. a season or year).

In order to successfully model a species, and practically apply that model in management, the data used in modelling must be as accurate and precise as possible These results served to demonstrate the importance of sampling accuracy and emphasised that researchers need to consider carefully the size and frequency of samples (weekly variation). Seasonal and yearly diet variation, suggest that planning the timing of sample collection is important, and regional variation that the area of sample collection should also be considered.

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Chapter 1:

General introduction and literature review

Chapter 1

SNOEK LIFE HISTORY

Snoek, *Thyrsites atun*, are found in temperate shelf waters throughout the Southern Hemisphere. They occur off the coasts of southern Australia, New Zealand, Chile, Argentina, the southern and south-western coasts of Africa, as well as several oceanic islands (such as Tristan da Cunha, Amsterdam and St. Paul) (Crawford, 1989b). In the Benguela ecosystem, snoek are considered important predators of pelagic fish stocks, as well as being commercially valuable (Griffiths, 2002). It was initially believed that the snoek in southern Africa comprised a single stock that underwent yearly long-shore migrations between Namibian and South African waters (Nepgen, 1979; Crawford and de Villiers, 1985; Crawford, 1989b; Griffiths, in press and 2002). This thinking came about as a result of tagging studies indicating a southward movement of tagged fish from Namibia to South Africa in autumn and winter, and catch statistics indicating apparent seasonal patterns of availability of snoek in South African waters. Recent studies indicate that the movements of the fish observed in the tagging studies were probably a result of offshore spawning migrations, and that the apparent seasonal availability to fisheries was because snoek are generally not fished during winter due to bad weather conditions. Present thinking is that snoek occurring in this system comprise two separate sub-populations, one off Namibia and the other off South Africa, with limited medium-term (ca 5 years) exchange between the two (Griffiths, in press). The life history of the South African stock has been comprehensively documented by Griffiths (in press and 2002), and aspects of this study are summarised briefly below.

Adult snoek are found throughout the distribution range of the species and long-shore movement appears nomadic and not subject to seasonal influence, except during times of spawning. Spawning occurs offshore (150 – 400 m isobaths) during winter and spring (May - November). Spawning grounds encompass the southern tip and western edge of the Agulhas Bank, and the West Coast as far north as Hondeklip Bay (Fig. 1.1). Egg and larval distribution corroborate the proposed spawning distributions, occurring offshore in the same geographical

range, between the 200 and 600 m isobaths. In Region 3 (Fig 1.1), where sex ratios are skewed during the spawning season, males appear to spend the majority of the spawning season on the offshore spawning grounds. Females are serial spawners and between spawning events, are thought to migrate inshore (landwards of the 150 m isobath) in this region, in order to feed on pelagic clupeoids. These prey species are more plentiful here, and offer more nutrition to the spent females than would the hake and other resources usually prevalent offshore. (Griffiths, in press and 2002).

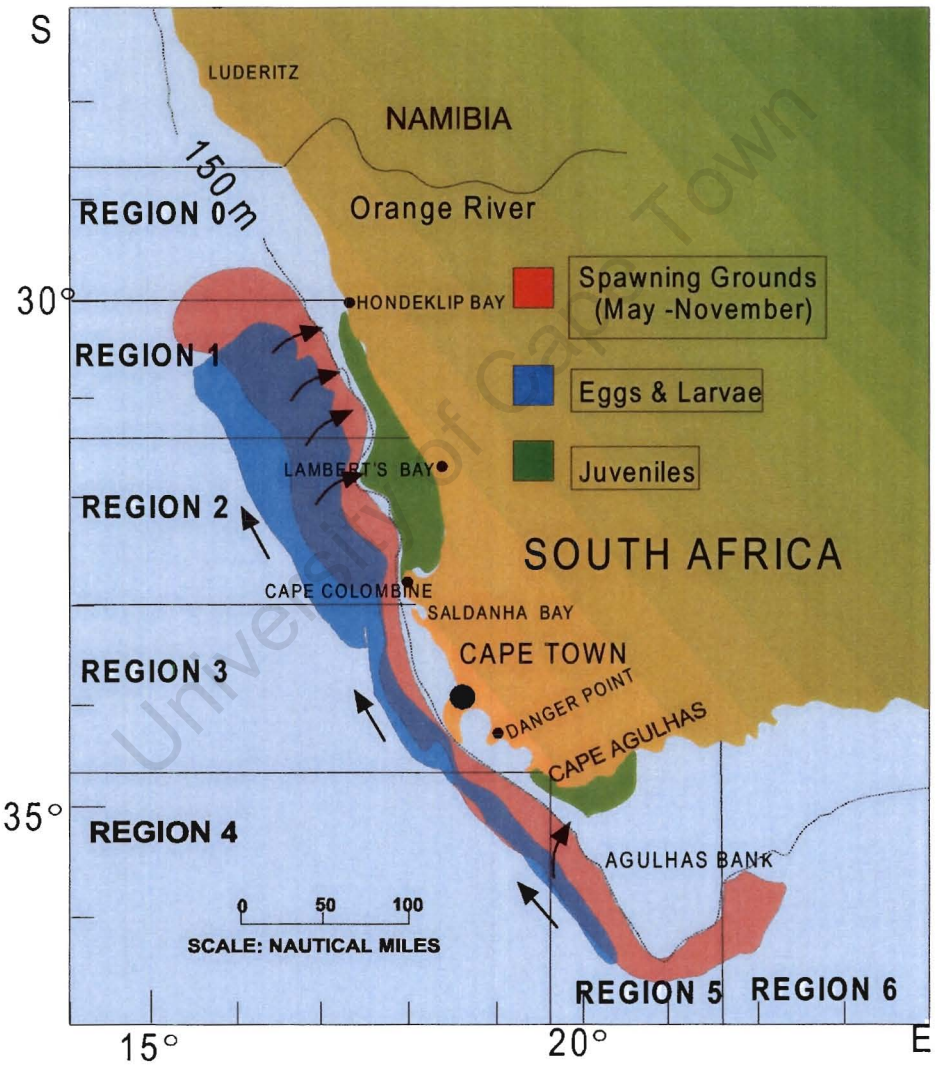


Figure 1.1: Map showing snoek distribution, spawning grounds and nursery areas. Sampling regions 0 - 6 are also indicated. Black arrows indicate current patterns and egg and larval movement (After Griffiths, 2002).

Currents transport eggs and larvae to nursery grounds. The principal nursery ground lies north of Cape Columbine and a secondary area is located east of Danger Point (Fig. 1.1). Early juveniles (5-24 cm) tend to remain inshore (< 150 m) in the nursery grounds, and may shoal with pelagic fish, which they begin to feed on as they grow larger (Griffiths, 2002).

Adult snoek are targeted by the commercial line-fishery in South Africa, where they are by far the most important species caught in terms of landed weight, with 6000-7000 tons line-caught caught and 4000 – 8000 tons trawled annually from 1996 - 1999. Line-fish catches are made inshore of the 150 m isobath and trawled catches are made by demersal trawlers, operating offshore, between the 150 and 400 m isobaths (Griffiths, 2002).

THE IMPORTANCE OF DIET STUDIES

The survival, growth and reproductive success of an organism are dependent on its success in obtaining sufficient food to satisfy its energetic and nutritional needs (Wooton, 1990; Lagler *et al.*, 1977). It follows that the feeding behaviour and diet of an animal are critical components of its life history. A knowledge of the diet of an organism is not only vital in understanding the biology of that organism, but also in the understanding how and where it fits into the ecosystem in which it occurs (Windell and Bowen, 1978; Berg, 1979; Amundsen *et al.*, 1996). The study of an organism in terms of its diet and feeding biology is known as trophodynamics. The trophic position, feeding behaviour and location, or 'role' in the system, determine the 'niche' it occupies. Information on the niche occupied by an organism allows speculation on its interactions with other organisms. Examples include competition, where the niches of two or more species overlap, and predator prey interactions: the species it consumes, and those for whom it is a food source (Begon *et al.*, 1990; Amundsen *et al.*, 1996; Hollowed *et al.*, 2000).

The food chains in most marine environments contain a series of links, which make up a complex food web. Typically, the lower trophic levels are characterised by a large number of planktonic species: phytoplanktonic producers, and zooplanktonic primary consumers. In

upwelling regions, such as the Benguela upwelling system, an intermediate trophic level exists, comprising small plankton–consuming fish such as clupeoids and engraulids, typically dominated by very few species. The higher trophic levels are again more diverse, containing many species of predators, from mammals and seabirds to predatory fish (such as snoek) (Cury *et al.*, 2000). Studies of the food consumption and diet composition of organisms or groups of organisms in such a system allow the construction of trophic models of the ecosystem, which are not only valuable scientifically, but are extensively practically applied in species and ecosystem management (Palomares and Pauly, 1989, Hollowed *et al.*, 2000; Whipple *et al.*, 2000).

Applications of predator diet studies

The large schools of small pelagic fish in upwelling systems, as well as many of the larger fish which prey on them, are valuable resources of significant economic importance to man (Tody, 1979). The three most important population regulation parameters used in the construction of holistic ecosystem models are predation (natural and fisheries removals); competition and environmental variability. A fishery is characterised by Dickie (1979), as a complex organisation that converts a supply of biologically produced material into a marketable product. In order to manage such a system, input and output dynamics need to be quantified and expressed in an understandable form (Dickie, 1979). Fisheries are often represented in models as consumers (fulfilling the same role as top predators) and they therefore compete with the natural predators in the ecosystem for the resource.

Modelling

Successful management of fishery resources, as with all natural resources, comes through a thorough understanding of the ecology and population biology of the species being exploited, as well as the functioning of the ecosystem in which they occur (Duffy *et al.*, 1985). Most fisheries management tools utilise mathematical single species models at present, which describe population growth, mortality and so forth. There is, however, a growing trend favouring the

introduction of multi-species models into this role, which allow a more detailed examination of the trophic interactions within the ecosystem in question. These require data, most notably from growth and diet studies, on all the species in the system about which the biological parameters are known (Whipple *et al.*, 2000). As predation is recognised as a fundamental structuring process in any ecosystem, predator-prey interactions (including predator diet and selectivity, prey abundance, diet switching, etc.), and the effects of fisheries must be studied and quantified for successful model construction (Hollowed *et al.*, 2000). The most effective ecosystem models are generally considered to be holistic, dynamic, multispecies models such as ECOSIM or MSVPA (Multispecies Virtual Population Analysis) (Hollowed *et al.*, 2000; Whipple *et al.*, 2000). This is because, unlike single species models, they permit the inclusion of predator removals as well as fishery removals. The dynamic multispecies approach also allows for predictions of the consequences of disturbances to one or more species on others in the system. Whole-system comparisons which include predator-prey and other species interactions, fishery harvest and the effects of changes in fishing pressure, can be undertaken using such models, allowing a degree of predictability and security in ecosystem management (Whipple *et al.*, 2000).

Diet studies can be used to provide estimates of how much, and how frequently, a predator eats. Obtaining variables such as differential digestion rates of prey species, and calculating daily rations for predators is undertaken for some species, using feeding trials (Hyslop, 1980). When these data are extrapolated for the population as a whole, total food intake for that population can be estimated. Such estimates can be used in the calculation of the natural mortality rate of prey species (Pauly, 1998). This can be modelled to assess the ecosystem effects of fishing, i.e. the impact of fisheries removals on the predator populations and the impact of predators and fisheries on prey populations. In addition, the degree of niche overlap (i.e. competition) between predatory species and between predators and fisheries can be assessed, as well as the impact of predator removals of the resource on fisheries (Crawford *et al.*, 1992; Hollowed *et al.*, 2000; Whipple *et al.*, 2000). There is a need for an understanding of the essential components in the diet of predators comprising valuable fisheries or conservation

risks, so that the trophic balance necessary for their survival can be maintained through careful management (Begg and Hopper, 1997).

Other applications

There are numerous other applications of diet studies, both in management and scientific contexts. The diets of predators in the Benguela ecosystem have been used as measures of prey abundance and distribution. For example, prey proportions in Cape Gannet (*Morus capensis*) diets were found to closely correlate with the abundance in the environment of their main prey species, most notably pilchard (Crawford *et al.*, 1992). Studies of the diets of predators can also provide valuable insights into their adaptive responses to the environment, and to the variability in available resources. Knowledge of how their behaviour and foraging habits are influenced by habitat, prey preferences, seasons, water temperature, prey movements, etc, can enrich our knowledge of adaptive mechanisms (Persson *et al.*, 1997). Studies of traits such as diurnal feeding habits in species can be a useful tool in determining optimum times for sampling, or indeed, fishing, a particular species (Windell and Bowen, 1978). Similarly, behaviour patterns such as migrations are often linked to available food sources and foraging theory, and an understanding of such behaviour allows for more accurate predictions of the distribution and movements of a species (Begg and Hopper, 1997).

In summary, diet studies provide valuable information on the biology, ecology and behavioural adaptations of a species. Fish feeding patterns often reflect changes in natural systems. By linking foraging theory and practical management, we may attempt to quantify disturbance to ecosystems, whether it be natural or anthropogenic (Stouder *et al.*, 1993). The twofold ecosystem effects of fisheries removals, namely 'predation' and 'competition' with predators, can be assessed. In addition, information on the diets and trophodynamic interactions of fish in marine systems are invaluable in the construction of ecosystem models and management tools, vital to maintaining the trophic balance of exploited species in natural systems (Pauly, 1998).

HOW DIET STUDIES ARE CONDUCTED

Practical sampling

The most widely used method for determining the diet composition of a fish species in the field is through stomach content analysis. For the most part, this necessitates killing the animal immediately after capture and preserving either the whole fish, or just the gut, as soon as possible, in order to prevent post-mortem digestion. Ideally, dissection should occur immediately after capture, but as this is often not possible in the field, stomach samples can be preserved by freezing, or storage in formalin or alcohol (Hynes, 1950; Windell and Bowen, 1978; Duffy and Jackson, 1986). Of these storage methods, freezing is preferable, despite the fact that samples tend to decay quickly after thawing. Storage in alcohol or formalin present certain problems: formalin preserves soft tissues well, but quickly dissolves hard tissues such as otoliths, while alcohol preserves hard parts, but does not preserve flesh effectively. Added to this, if the samples are to be analysed according to mass, preservation in alcohol or formalin may render results inaccurate, as subtle changes in mass may occur during storage time (Duffy and Jackson, 1986).

In order to give a more accurate idea of the food actually consumed, the examination of the digestive tract is usually restricted to the stomach and oesophagus. Digestion is usually less advanced in the stomach than further down the tract and the prey items here, being more intact, are generally easier to identify (Hynes, 1950; Duffy and Jackson, 1986). Examination of the stomach alone also serves to reduce the effects of the time of passage of food through the gut, such as the differential rates of digestion of prey items, which tend to be compounded with time. Differential prey digestion rates are a notable source of error in stomach content analysis (Hyslop, 1980). Prey with soft bodies, or a low mass and high surface area are subject to quicker digestion rates than those with a more dense structure, leading to an underestimation of their contribution to the diet. Prey items with hard structures, such as otoliths (fish), chitinous shells (crustaceans) or beaks (squid) may be overestimated in analysis, as these parts tend to remain behind long after digestion of the prey body has occurred (Berg, 1979; Hyslop, 1980). There is no way to effect compensations for this error in field studies, but *in vitro* determinations

of digestion rates for various prey types can be applied to correct for differential rates (Hyslop, 1980).

Prey items in the stomachs are identified to the lowest possible taxon. In the case of abundant prey, it is preferable that species are identified, whereas rare or uncommon prey may simply be grouped according to family or class. When the food items are at an advanced stage of digestion, they are often impossible to identify and thus it is necessary to make certain assumptions. The unidentifiable material can either be ignored, it can be treated as a discreet prey group, or the assumption can be made that its composition is equivalent to that of the identified prey. This last assumption is likely to be inaccurate, as the different stages of digestion would suggest different feeding events, and thus possibly different prey types (Duffy and Jackson, 1986). Ignoring unidentifiable foodstuffs may lead to bias against material that is more readily digestible, therefore, the method recommended by Duffy and Jackson (1986), as making the fewest assumptions, is that unidentified prey is treated as a separate food group. It is nevertheless possible in most cases to assign unidentified prey to broad taxa, e.g. fish, squid, crustacean.

Analysis of stomach content data

There are many methods for analysing and presenting stomach content data and there is little consensus in the scientific community as to the optimal manner in which this should be done. All the techniques employed have both positive and negative attributes, and rather than searching for one perfect analytical tool, it is perhaps preferable to choose an analysis suited to the purpose of the study in question (Duffy and Jackson, 1986). Listed below are some of the more commonly used methods for analysis of dietary data, with comments on their benefits and drawbacks.

1. Frequency of occurrence (% Occurrence): This is defined as the percentage of the total number of stomachs (containing food) in which a specific prey type occurs (Hyslop, 1980;

Amundsen *et al.*, 1996). This technique has the advantage of being quick to execute, the researcher merely recording the presence or absence of prey (Duffy and Jackson, 1986). It provides information on the proportional contributions of prey items to the predator population, but provides no information on the biomass or numbers of each prey type consumed. It is also biased toward prey items that are less easily digested, and those that occur frequently, but in low numbers in individual stomachs (Hyslop, 1980; Windell and Bowen, 1978).

2. Numerical percentage (% N / % Abundance): The number of individual prey items for each prey type in each stomach is counted, and expressed as a percentage of the total numbers of all prey items (Hyslop, 1980; Windell and Bowen, 1978). As with the frequency of occurrence method, this technique provides no information on the biomass of organisms present in the diet. It also tends to over-represent small, abundant prey items over large, scarce ones. It is therefore generally only recommended for use where prey items are of a more or less uniform size. In addition, the technique is only useful where prey are consumed whole. Where only prey parts are eaten (e.g. by scavengers), diet composition cannot be estimated with any accuracy. The state of digestion also influences accuracy here, as individual prey items are much harder to count once their structural integrity has begun to deteriorate (Hyslop, 1980; Duffy and Jackson, 1986).

3. Percentage mass (% M / % Weight) and percentage volume (% V):

%M: Prey items are weighed either in a wet state or are dried and then weighed. Mass values for each prey type are summed and expressed as a percentage of the total prey mass (Windell and Bowen, 1978; Hyslop, 1980). Wet mass is a much easier measure to use than dry mass, which necessitates the use of drying equipment. This process is time consuming, especially where large samples are being analysed. There is a high degree of correlation between wet and dry mass, provided that wet samples are fresh or frozen. The exception occurs when mass changes have resulted due to storage in alcohol or formalin. To avoid invalid results, such samples may need to be dried (Duffy and Jackson, 1986).

%V: Prey volumes are measured by water displacement, by settled volume or even by % cover in a gridded sorting dish expressed again as a percentage of the total food volume (Windell and Bowen, 1978; Hyslop, 1980; Duffy and Jackson, 1986).

Mass measurements were used throughout this study, this because the advantages of using mass or volume are that the biomass consumed and nutritional contribution of prey to the diet can be estimated. Mass and volume measurements cancel the effects of numerous small prey items in the numerical method, but they do tend to overemphasise large, rare prey items in the diet, particularly if sample sizes are small (Windell and Bowen, 1978; Duffy and Jackson, 1986; Cortes, 1997). Differential digestion rates may present a source of error in these methods. Correction factors may be employed in such cases in order to estimate pre-ingestion mass of these prey items, for example, calculating of the original prey size from the dimensions of hard structures, such as the claw of a crab or a fish otolith, etc. However, presentation of such measures must be carefully approached, to avoid compounding error (Duffy and Jackson, 1986).

Volume and mass measurements may also be used in the calculation of the consumption index C or stomach 'fullness', where:

$$C = \frac{\text{Weight of food in stomach}}{\text{Fish weight}} \times 100 \qquad \text{.....equation 1.1}$$

The consumption index can reveal patterns in the feeding habits of the fish, such as diel feeding cycles or seasonal variation of food intake (Hynes, 1950; Berg, 1979; Hyslop, 1980). In using mass and volume measurements, it is important to specify whether the empty stomachs in the sample are included in the calculations. If one is merely calculating percentage composition of prey types, it is usually not necessary to include empty stomachs in analysis. In observing fish feeding habits, at the population level, the numbers of empty stomachs can be factored into consumption estimates in order to reveal patterns in foraging behaviour.

4. Compound indices: These are designed to correct for the sources of error introduced in the individual analytical techniques described above. Two or more of the abovementioned measurement techniques are undertaken on the sample, and incorporated into an equation, intended to give a more accurate representation of the diet. The most commonly used compound index is the Index of Relative Importance (IRI), developed by Pinkas *et al.* (1971), where:

$$\mathbf{IRI = (\%N + \%V)\ x\ \%F} \qquad \text{.....equation 1.2}$$

(**N** is the numerical percentage, **V** the volumetric percentage and **F** the frequency of occurrence) (Hyslop, 1980). This method of analysis reduces the biases that occur in the numerical, volumetric and frequency measurements, caused by many small or few large prey items (Duffy and Jackson, 1986; Cortes, 1997). Two other less common indices include the Absolute Index (AI), which gives equal weighting to all three measurements (% M – percent mass, % V and % F), and the Relative Importance Index (RII), where the prey items are ranked against each other instead of against a fixed scale (Duffy and Jackson, 1986).

The merits of compound indices have frequently been called into question. They are not accepted as infallible and are not in universal use, meaning that comparisons between studies are not always possible. Being derived, the values of the AI and the IRI are essentially meaningless, unless used in comparison. The RII is infrequently used as it involves complex computation (Duffy and Jackson, 1986; Cortes, 1997). Hyslop (1980), states that "such indices can confound two sources of error and variation", and in the case where three measurements are used, the error is presumably further compounded. MacDonald and Green (1983) proved, using Principle Component Analysis (PCA) in several fish communities, that the various diet measurements correlated very closely, rendering the compound indices redundant. Essentially the use of these indices requires a great deal more time in sample analysis, since it is necessary to obtain three measurements. They are also often clumsy to calculate, and do not actually increase the amount of information gained (MacDonald and Green, 1983).

Hynes (1950), sums up this sentiment succinctly in stating " ...for any fish with a generalised diet, provided a large number of specimens are examined, any of the commonly accepted methods of assessing the composition of the diet...from gut contents will give substantially the same result. Those ...items important in the diet will always stand out clearly from those that are occasional or rare...and the variation between the different methods will probably not be greater than between different samples of fish".

Feeding strategy and graphic representations of diet

A new analytical method proposed by Costello (1990), was the use of a graphic presentation of fish diets, in a manner that provided information on both the diet and feeding strategy of a species. He recognised that graphic representations of diet are easier to interpret and understand than, for example, summary tables (Costello, 1990; Cortés, 1997). These methods are of great importance in describing diet, and in particular, feeding strategies. Two diet measures are plotted on the x and y axes of a two-dimensional graph (Figure 1.2), namely % Occurrence (the percentage of predators in which a prey type occurs) and % Abundance (or %N, the total numerical percentage the prey type makes up of all prey types encountered).

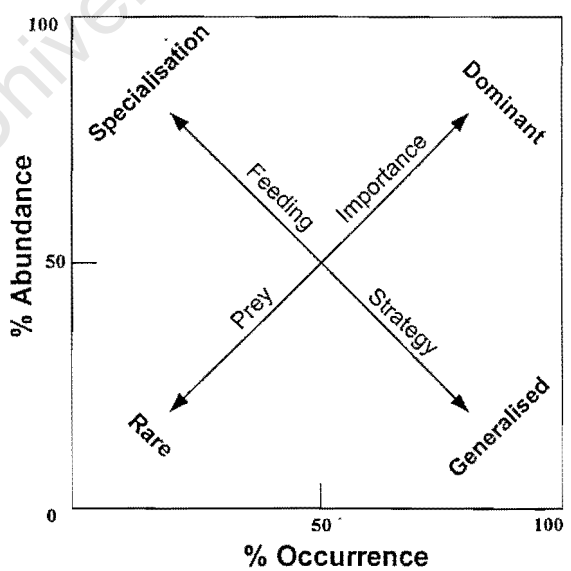


Figure 1.2: Explanatory diagram for Costello's graphic representation of diet and feeding strategy **(After** Amundsen *et al.*, 1996)

Two diagonals representing diet and feeding strategy bisect the graph. The 'prey importance' diagonal from bottom left ('rare' prey) to top right ('dominant' prey) indicates the dietary importance of the various prey types. The 'feeding strategy' diagonal from top left (specialisation) to bottom right (generalisation) indicates the degree of diet specialisation in a species. For example, prey data points that fall in the lower right-hand quadrant of the graph indicate species that are consumed often but in small numbers, i.e. generalist feeding by the predators; whereas data in the upper left-hand quadrant appear in large amounts in only a few fish, indicative of specialisation. This technique allows a more detailed analysis and understanding of the feeding behaviour of fish. It has been subsequently modified by two authors.

Cortés (1997) modified the structure of the graph to produce a three-dimensional representation of diet and feeding strategy, employing % Occurrence, % Abundance and % Weight. The descriptions of feeding strategy are essentially the same as in Costello's (1990) method, however allowance is made for the bias introduced by the size and weight of prey items. For instance, if prey points cluster around the % Weight axis, then their mass must contribute more than their numerical count, and vice versa. Although this method served to reduce size and mass-based bias, it did not essentially modify Costello's (1990) ideas.

A more in-depth modification of the technique was suggested by Amundsen *et al.* (1996). This method took into account theoretical considerations of optimal foraging, competition and niche-breadth theories, and the results gained, produced a far more detailed account of the actual feeding strategy of the fish. It was noted that in Costello's (1990) graph, a generalised diet need not only occur at the bottom right of the figure (Figure 1.2) but could, in fact, occur along the entire length of the x-axis, due to variations in niche breadth within a population. Thus, two previously unconsidered sources of dietary variation were introduced to Costello's (1990) method, giving a more accurate graphical representation of diet and feeding strategy. These additional sources of variation were considered essential in determining the niche breadth of a species or population. The first referred to the variation in the diet and resource utilisation of an

individual (the within phenotype component – WPC), and the second referred to the variation in resource use and niche breadths between all the individuals of a population (the between phenotype component – BPC). The separation and analysis of these components is made possible in this modified graphic representation of feeding strategy.

Instead of plotting % abundance, a new parameter is added, namely, 'prey-specific abundance', which is plotted on the y-axis, and is given by the formula:

$$P_i = (\Sigma S_i / \Sigma S_{t\,i}) \times 100 \qquad \text{.....equation 1.3}$$

Where P is prey-specific abundance; S_i is the percent (number, mass or volume) stomach content of prey type i; $S_{t\,i}$ is the total stomach content in only those predators with prey type i in their stomachs.

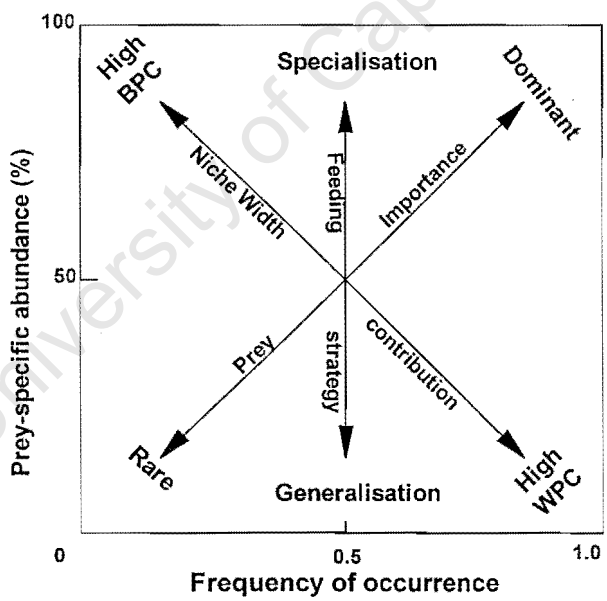


Figure 1.3: Explanatory diagram for the modification of the Costello method by Amundsen *et al.* (1996), allowing for interpretations of feeding strategy, niche breadth and prey importance (After Amundsen *et al.* ,1996).

The product of prey-specific abundance and frequency of occurrence can be represented on the graph as total area per prey type, drawn as isopleths for each prey species. The graph is again divided by the two diagonals, but is vertically bisected as well (Figure 1.3). The 'prey importance' diagonal from the lower left (rare) to upper right (dominant) as in Costello, indicates the significance of the various prey items. The 'feeding strategy' line is vertical with the upper

end indicating specialisation and the lower end, generalisation. The other diagonal, 'niche width contribution' extends from the lower right (high WPC – within-individual variation in resource use) to the upper left (high BPC – variation between individuals). The detailed nature of this graph allows an in-depth analysis of feeding strategies and niche widths of populations and individuals. Conclusions on generalisation and specialisation, as well as the variation in resource use by individual fish and the population as a whole can be gained from these graphic representations. These methods were not used in this study, as feeding strategy was not investigated due to time constraints, but they are considered important for future research on this species.

Food consumption studies

Stomach content data can provide vital descriptions of the trophic role of an animal, but reveal little quantitative information about how much is consumed. In order to model population consumption, it is necessary to determine how much an individual organism ingests over time (Palomares and Pauly, 1989). There are two well-known methods for obtaining the necessary data: estimates of consumption in the wild, and captive feeding experiments. A third method, based on theoretical relationships, has also been developed.

Food consumption data are hard to obtain in the field, and generally involve making subjective assumptions. One technique suggested is to sample daily, and assume that the average amount of food in the stomachs of a sample of fish could be used to estimate daily ingestion rates. The assumptions made here are that food consumption is continuous throughout the day, or that fish only feed once per day, and that digestion rates are constant over time and for all prey types (Windell and Bowen, 1978; Palomares and Pauly, 1989). The data obtained in such studies tend to be highly variable and contain many potential sources of error, especially where small samples are used. This, combined with the use of untenable assumptions, mean that these methods are at best questionable, at worst, highly inaccurate. Accuracy can be improved by sampling fish over a 24hr period to determine when they feed and how much food is consumed (Jenkins and Green, 1977). This presents problems, however, as feeding may vary

from day to day, between seasons and according to prey densities (Eggers, 1977; Wooton, 1990).

Captive feeding studies generally provide far more accurate estimates of actual consumption and digestion rates (Wooton, 1990). Fish in aquaria are fed known rations and are then sacrificed at various times after ingestion in order to obtain estimates of stomach evacuation rates (Swenson and Smith, 1972). Evacuation rate is defined as the amount of time taken for the passage of all food in the stomach into the intestine (Windell and Bowen, 1978). Using evacuation rates, daily ration values are calculated and estimates of consumption are then calculated using the ration values (Palomares and Pauly, 1989). Consumption rates can also be calculated if the food conversion efficiency of a fish species is known. This involves studying how the energy consumed by the fish is used, i.e. what percentage is used for growth, reproduction, respiration, etc., and converting these data into consumption estimates (Elliot and Persson, 1990; Wooton, 1990). Modern equipment allows researchers to vary experimental conditions and ideally to reproduce conditions as close to the natural environment as possible (Wooton, 1990). In addition, mathematical corrections incorporating multiple regressions can be employed to rectify the differences between results from fish in captivity and in nature, further improving accuracy (Palomares and Pauly, 1989). Laboratory studies can present the problem, however, that fish are usually fed 'ad lib', with the result that they may consume far more than is available to them in nature, thus bringing accuracy into question (Windell and Bowen, 1978).

In cases where the fish are too rare to sacrifice, other methods have been developed to study digestion rates. Examples include stomach pumps, which extract food from the stomach at various stages of digestion, the use of emetics (drugs which induce vomiting), or simply removing food from the stomach with forceps (Hyslop, 1980). An X-ray technique has also been used, but this is suitable only in the case of piscivorous fish, where the prey fish of a narcotised fish is observed and timed as it is digested (Windell and Bowen, 1978). The trouble with some of these techniques is that they are invasive to the study animal, and the resultant trauma could affect digestion rate (Hyslop, 1980).

Pauly (1989) notes that consumption rate is one of the most difficult and costly parameters to estimate in terms of modelling. Apart from the inaccuracy of field studies and the need for expensive equipment, not all fish species can be conditioned to a laboratory environment. Realising the need for alternative methods to estimate consumption rate, Pauly has developed a theoretical, mathematical model, which aims to achieve this objective (Palomares and Pauly, 1989; Pauly, 1989).

Pauly's model incorporates the four parameters that he surmised contribute most to consumption rate. These are $W\infty$, the asymptotic weight of the species; **T**, the average habitat temperature; **F**, the food type consumed (with values of 0 for carnivores and 1 for herbivores) and **A**, the aspect ratio of the caudal fin. Aspect ratio is a species-specific constant that correlates closely with the activity level of fish. It has been observed that very active fish with high metabolism and therefore high consumption and evacuation rates have a high aspect ratio. Slow moving, inactive fish with lower consumption rates tend to have low aspect ratios. **A** is given by the equation:

$$A = \frac{h^2}{S} \qquad \text{.....equation 1.4}$$

Where **h** is the height of the caudal fin, and **S** is its surface area: The use of **A** as an activity index implies two things. Firstly that the shape of the caudal fin has been optimised over evolutionary time in accordance with the physiology of the fish, to give the most efficient propulsion possible for its feeding strategy. Secondly, that the model only applies to fish with scombriform locomotion, where the caudal fin is the main means of propulsion. The model produces a result in terms of consumption per unit fish mass or **Q/B**:

$$\ln Q/B = -0.1775 - 0.2018 \ln W\infty + 0.6121 \ln F + 0.5156 \ln A + 1.26F \text{ (0 or 1)} \qquad \text{.....equation 1.5}$$

This model explained nearly 75% of the variance observed for 33 fish species, and seems a truly viable method for the estimation of consumption rate, where practical methods cannot be used (Palomares and Pauly, 1989; Pauly, 1989).

In conclusion, the methods relating to diet studies are many and varied, ranging from very simple to highly complex. For management purposes, it is preferable to obtain as accurate and precise an idea of the diets and consumption rates of as many species as possible, in order to understand and model ecosystems effectively. Whatever the methods chosen for a study, they must be carefully outlined and must ultimately be chosen to correspond with the aims of the study.

A REVIEW OF PREVIOUS SNOEK DIET STUDIES

Physiology and feeding habits

Snoek are elongated fish with a smooth silvery appearance. They reach a maximum total length of about 1.5 m, corresponding to a mass of 9 kg (Blackburn and Gartner, 1954; Griffiths, 2002). Sexual maturity is reached at an age of roughly 3 years, and a fork length of 75 cm (Griffiths, 2002). They have powerful jaws and sharp cutting teeth that point inwards, indicating that prey are not masticated, but rather swallowed whole, or bitten in half and swallowed (in the case of larger prey). The stomach, typical of a predatory fish; is well defined, has a longitudinally corrugated inner lining and is able to expand to a considerable size. Strong acid secretions, along with the short digestive tract, suggest that digestion occurs rapidly (Keast, 1979; Nepgen, 1979a).

Snoek usually feed in large schools on pelagic schooling organisms, but are known to consume benthic species at times (Blackburn, 1956; Nepgen, 1979). Blackburn (1956), postulates that they undergo vertical migration, following prey species, at least once every 24 hours in Australian waters. In fact, standard fishing practice relies on their surfacing at daybreak, and less frequently, at sunset. They are virtually never caught after dark on the surface in Australian waters (Blackburn, 1956), but in South African waters, fishermen state that snoek are often caught on the surface at night. It is thought that in the Benguela ecosystem they follow the diel vertical migration patterns of their prey species, (e.g. pilchard, *Sardinops sagax*, and anchovy,

Engraulis encrasicolus), which move to the surface at night in order to feed on plankton (Crawford, 1989b; Van der Lingen, 1999).

Snoek feeding behaviour has only ever once been documented, in Australian waters. The fish were feeding on a swarm of euphausiids at the surface of the water. They were observed swimming around the swarm, 'herding' the krill into a tight 'ball', which they would then attack, swimming in with their mouths open (Blackburn, 1956). Whether this behaviour occurs in South African snoek is not known, although it is consistent with the known hunting tactics of many schooling predators (Wooton, 1990).

Previous studies

One of the first studies undertaken on snoek in South Africa was a tagging study conducted in 1934 and 1935 by Marchand (Marchand cited by de Jager, 1955). The results of this study led to the theory that snoek exhibit annual migrations between Namibian and South African waters. Davies (1954), noted that snoek were important predators of pilchard and maasbanker (*Trachurus trachurus capensis*), but did not conduct an in depth diet study. De Jager (1955), further discusses snoek migration patterns and their role as predators of pilchard, but his study focused mainly on the developmental stages of the eggs (de Jager, 1955).

Nepgen (1979a and 1982) conducted the first in-depth study on the diet of snoek between 1958 and 1974. Stomachs from 2 815 line-caught and 156 trawl-caught fish were examined over this time. Between 70 and 250 stomachs were examined each year, of which 35% to 92% contained food. Nepgen lists 29 species found in the diet, including fish, crustaceans and cephalopods, according to the frequency of occurrence in the stomachs. The most common foods in the line-caught fish were anchovy (*Engraulis encrasicolus*), pilchard (*Sardinops sagax*), maasbanker (*Trachurus capensis*) and mantis shrimps (*Pterygosquilla armata capensis*). Trawl-caught fish were found to contain higher percentages of hake (*Merluccius spp.*), euphausiids (*Euphausia lucens*) and lantern fish (*Lampanyctodes hectoris*). The diet composition in line-caught fish was found to change from year to year, and Nepgen explained this as being linked to the availability

of prey species (Nepgen, 1979a). An additional study was conducted in False Bay from 1979-1980, where anchovy and pilchard were again found to be the main prey types, however, diet analysis was again restricted to frequency of occurrence data (Nepgen, 1982).

In a third study, Crawford and de Villiers (1985) used the same data gathered by Nepgen between 1958 and 1980. Their aims were to link snoek migrations to prey movement and availability, notably to pilchard and anchovy spawning migrations. The study did not investigate the diet diversity and composition, but rather how snoek diet, feeding behaviour and availability to the hand-line fishery were linked. The link between natural mortality of prey, variability in their biomass and distribution, and predation by snoek was also explored.

Data on snoek abundance were obtained from annual catch statistics from the hand-line fishery. The diet was quantified, mostly around the Cape Peninsula, where the frequency of occurrence of anchovies in the diet was recorded for the samples of 6 – 1 068 fish per annum. Due to low sample sizes, a three-year moving average was used for some years. This study was largely based on three assumptions. Firstly that snoek exhibited north to south migrations in autumn and winter, from Namibian to South African waters. Second, that the hand-line catches of snoek were an accurate measure of their abundance and the extent to which they were preying on anchovy, and third, that the period during the year that snoek feed on anchovy remains constant.

Crawford and de Villiers' (1985) findings were that snoek appeared most abundant off the west coast of Namibia around Walvis Bay in summer, and were caught further south, between Lamberts Bay and Cape Point in winter and spring. Off the Western Cape, they linked the southward movement of snoek to the movement of juvenile anchovies and pilchards southwards from St. Helena Bay (late autumn) to east of Cape Point (winter to spring). They postulated that the snoek moved offshore in the western Cape after winter, when there a massive decrease in prey abundance was thought to occur. Fish trawled offshore at this time were found to consume round herring (*Etrumeus whiteheadi*) between winter and late summer,

and euphausiids in spring. This reduction in prey availability was thought to trigger the offshore movement/ northward migration of snoek, reflected in decreased catches after winter.

Catches of snoek were related to catches of anchovy by the purse-seine fisheries and guano production, where two correlations were noted. First, that high guano production coincided with high snoek catches in the 1890's and 1920's, and that good hand-line catches in 1976 coincided with exceptional purse seine catches. The effect of snoek predation on the natural mortality of anchovy was inferred by the relationship between hand-line catches of snoek, and the VPA (virtual population analysis) estimates of anchovy biomass (Crawford and de Villiers, 1985).

The fourth study of snoek diet made up one component of a Master's thesis produced by Dudley (1987), which was a study of the biology, distribution and catch trends in snoek. An unspecified number of trawls and line-caught samples were used to produce inshore and offshore diet descriptions. Feeding periodicity and behaviour were also investigated using biannual demersal trawl data and mid-water trawl data. Samples (of unspecified size) were gathered over three years (1983-1986), and over a wide geographical range (Cape Point to Luderitz), and a total of 380 stomachs containing food were used to describe the diet over this period. Differences between the inshore and offshore diets were noted, with the most important inshore prey item being anchovy (*Engraulis encrasicolus*), and the most important offshore item, red eye roundherring (*Etrumeus whiteheadi*). Offshore diet was found to be more diverse than inshore diet, and included species such as hake, lightfish (*Maurolicus muelleri*) and lanternfish. Notable, in comparison to studies before and since, was the virtual absence of pilchard from the diet. Dudley attributed this to low pilchard abundance over the period of the study (Dudley, 1987).

Inferences were made on the seasonality of prey availability offshore, as demersal trawls were undertaken biannually (July – winter, and January – summer). The relative importance of prey differed from summer to winter, but these differences were not described in detail, apart from

the fact that anchovy and pilchard were absent from the diet in summer, and that garfish (*Scomberesox saurus*) was absent in winter.

Stomach fullness indices and the degree of digestion for trawled samples of ten stomachs each, were used to investigate feeding periodicity and the depth at which feeding occurred. No clear feeding periodicity was noted, and feeding was concluded to be continuous throughout the diel cycle with slight peaks in the afternoon. Dudley concluded that feeding took place throughout the water column, although he concedes that mid-water trawls may have produced biased results, as they were specifically targeting tight shoals of clupeoids, which would have attracted feeding snoek. Although no trawled catches were made after dark, he did suggest that vertical feeding migrations might occur at night in snoek (Dudley, 1987).

Griffiths (2002) conducted the fifth and most recent dietary analysis of snoek between 1994 and 1997, as part of a life history study. Data were pooled over the four year period, but divided into fish line-caught inshore of the 150 m isobath and trawled offshore. Inshore data were also divided into four size classes of snoek: 5 – 24 cm (early juveniles, n=11); 25 – 49 cm (juveniles, n=212); 50 – 74 cm (sub-adults, n=540) and >74 cm (sexually mature adults, n=1069). Offshore data included only the two larger size classes, sub-adults (n=195) and adults (n=569). Diet was estimated according to percent frequency of occurrence, as well as percent (wet) mass. These were combined into a compound index, namely the IRI (Index of Relative Importance), which was then converted to %IRI.

The study revealed that snoek consume both demersal and pelagic prey, which included 22 species of teleosts, nine species of crustaceans and six cephalopod species. The inshore samples showed that marked ontogenetic diet shifts occur, with crustaceans dominating the early juvenile diet, decreasing in importance with the growth of the snoek. The study indicated that early juveniles, inshore of the 150 m isobath, feed largely on lantern fish (*Lampanyctodes hectoris*), euphausiids (*Euphausia lucens*) and amphipods (notably *Themisto gaudichaudi*). Juveniles begin to feed on juvenile pilchard (*Sardinops sagax*) and anchovy (*Engraulis*

encrasicolus), as well as lanternfish and amphipods. The sub-adults continue to feed on these prey items, as well as euphausiids. The diet of adult snoek (> 74 cm; 50% sexual maturity, ca 3 years) is far more diverse, probably partly due to the movement offshore of mature individuals and the wider adult distribution. Adults also have a larger gape size, and therefore more options as to prey species, and in sampling adult diet, diversity was possibly increased by the larger sample sizes examined. It was found that pilchard, anchovy and mantis shrimps (*Pterygosquilla armata capensis*) were the most important prey items consumed by those adult fish caught inshore by handline, followed by maasbanker (*Trachurus trachurus*), chub mackerel (*Scomber encrasicolus*), and cephalopods (such as *Inioteuthis* and *Loligo vulgaris reynaudii*). Pilchard, round herring (*Etrumeus whiteheadi*), Cape hakes (*Merluccius spp*), lightfish (*Maurolicus muelleri*), lanternfish, ribbonfish (*Lepidotus caudatus*), saury and euphausiids were more prevalent in the diet of those fish caught offshore in demersal trawls.

This study also served to refute the migration theories regarding snoek. Griffiths showed that snoek are available to line-fishers off the South African coast throughout the year. It is now thought that the South African and Namibian stocks are separate, and although some migration may occur between the two, long-shore movement of the South African stock is essentially random, and only offshore spawning migrations have a seasonal basis (Griffiths, 2002).

LIMITATIONS OF THE PREVIOUS STUDIES: THE NEED FOR FURTHER RESEARCH

Sample size and analysis

The most problematic aspect of the diet studies conducted by Dudley (1987), Nepgen (1979a) (and Crawford and de Villiers (1985), using Nepgen's data) relate to the inadequate sample sizes used (Griffiths, 2002). For example, Nepgen employed a minimum sample size of six stomachs containing food, which are used to quantify the diet of snoek for an entire year. It is not feasible to represent the prey types in a fish diet using such low sample sizes. Dudley used a total of 380 stomachs containing food to describe diet over three years, and although the actual sample sizes used are not given in his thesis, it could be assumed that they were not

substantial. He did mention the fact that the sample sizes used in the feeding behaviour study were of questionable size (ten stomachs per trawl, including empty stomachs) (Dudley, 1987). The sample numbers employed for some years by these studies were only sufficient to reveal the presence or absence of the species consumed, and not to give any comprehensive quantitative representation of the diet (Duffy and Jackson, 1986). It is thus hard to make confident assumptions or effective comparisons based on some of these results.

Nepgen, and Crawford and de Villiers used only frequency of occurrence as a measure of prey proportions in the diet, which only provides a "crude qualitative picture of the food spectrum" (Hyslop, 1980). As indicated earlier, this technique tends to heavily bias against organisms that are easily digested, and toward small but numerous items in the diet. In addition, no information about biomass or numbers of prey is gained, merely a very broad idea of the presence or absence of species in the diet, and, at best, only a limited idea of the proportional contributions of each.

New discoveries

Initiatives like the Benguela Ecology Programme, a multidisciplinary investigation into the processes occurring in the ecosystem, have, over the past 20 years, greatly increased our understanding of the food webs in the Benguela, the interactions between species and the effects of the environment on recruitment and abundance of fish (Shannon *et al.*, 1992). Much new information has become known since the previous snoek diet studies were conducted, indicating that they were based on assumptions and theories that we now know to be untrue or inaccurate. One such assumption was that snoek migrate between South African and Namibian waters on an annual basis, and the resultant assumption was that snoek were only available in South African waters at certain times of the year. For this reason, sampling was only conducted when snoek were believed to be available around the Cape Peninsula, namely in summer and autumn. We now know that snoek are available to linefishers almost year-round in this area, although less may be fished in winter due to bad weather (Griffiths, 2002). The diet constructed was based on this limited sampling period, and may thus not be inclusive. Crawford and de

Villiers (1985) also assumed that the period of the year in which snoek feed on anchovy was constant. This would seem to imply that the diet changes seasonally, but there is no mention of what this change might involve, nor any attempt to substantiate the supposition.

It was Dudley (1987) that first proposed the idea of a resident stock of snoek, and Griffiths (2002) went on to prove that this was the case, and to refute the annual migration theory.

The study conducted by Griffiths (in press and 2002) added greatly to our understanding of snoek, with regard to both life history and diet. Sample sizes used were much larger than those in the previous studies, and the nursery grounds were sampled, providing information on ontogenetic diet shifts. The diet data were, however, pooled over four years and may thus have excluded trends associated with inter- and intra-annual temporal variation. Notwithstanding his small sample sizes, Nepgen's study did indicate that there were shifts in the proportions of prey types from year to year. The high diversity of taxa found in snoek diet indicate that they are generalist feeders, defined as organisms which utilise many prey types, but often favour a few items that make up the bulk of the diet. Generalist predators characteristically show opportunistic utilisation of available resources, and diet shifts are common as prey numbers fluctuate, e.g. through seasonal migrations (Keast, 1979). Because upwelling ecosystems contain so many influential and variable components, they are in a constant state of flux. Shifts in prey resources force the evolution of behavioural plasticity in their predators (Persson *et al.*, 1997), and as Stouder *et al.* (1993), state: "Variability in fish feeding ecology is the rule, rather than the exception." The previous studies on snoek do not adequately take into account all the possible sources of variation that could influence the diet. Duffy and Jackson (1986) note that diets can vary temporally (at many scales), between locations and between the sexes, sizes and ages of a species. The Benguela ecosystem is characterised by Smale (1992), as a patchily rich but unpredictable system, in which predation patterns are known to vary with time and locality.

Variation in the Benguela Ecosystem

The Benguela ecosystem is highly variable on time scales from hours and weeks to months, years and decades. The variation is not only environmental and climatic, but is reflected in

"substantial changes in the abundance or production of the key living resources" (Smale, 1992). Two species that form the principle components of the diet of snoek, namely anchovy and pilchard, are amongst the organisms whose abundance is least predictable and most variable.

At a decadal time scale, anchovy and pilchard are thought to undergo shifts in dominance in the system. This is a pattern noted in many upwelling systems where similar species co-exist (Roel *et al.*, 1994, Cury *et al.*, 2000). Pilchard dominated the Benguela in the early half of the last century, until a stock collapse in the mid 1960's. Anchovy was then dominant until the mid 1980's when pilchard numbers began to increase again (Roel *et al.*, 1994).

At a yearly or seasonal scale, pilchard and anchovy exhibit distinct fluctuations in abundance from region to region, as a result of spawning and recruitment migrations. Both species spawn over the Agulhas Bank, with peak spawning occurring in summer (Armstrong and Thomas, 1989; Roel *et al.*, 1994). Pilchard are thought to spawn year-round, and are found in highest concentrations on the western bank during summer. Anchovy spawning is restricted to spring and summer (Armstrong and Thomas, 1989; Barange *et al.* 1999). Jet currents transport the eggs and larvae up to nursery grounds on the west coast during summer and autumn, and recruits begin a southward migration back onto the Agulhas Bank, making them available inshore on the west coast during winter. These patterns of movement could mean seasonal and regional fluctuations in their availability to predators. In autumn, juveniles are available in nursery grounds north of Cape Columbine. In winter, recruits are found on the west and south coasts, and in spring and autumn they are concentrated on the Agulhas Bank (Armstrong and Thomas, 1989; Roel *et al.*, 1994; Shannon *et al.*, 1992).

Regional availability to snoek of these species may also change, depending on which is the dominant one in the system, as pilchard distribution extends further offshore than that of anchovy (Cury *et al.*, 2000). Another species found frequently in the diet of snoek, the round herring, displays a similar migration pattern to pilchard and anchovy (with peak spawning in late winter), and thus this species could also have a fluctuating availability (Roel *et al.*, 1994). Other

species found in snoek diet, also exhibit fluctuations in abundance according to location and season. Euphausiids and mantis shrimps, for instance, are found in much higher concentrations on the west coast in summer, during upwelling, whereas in winter they are found off the south coast (Pillar, 1986).

Previous studies have not taken into account the temporal fluctuations of prey resources in fixed areas, or the regional availability of resources over the distribution range of snoek. In addition, possible seasonal alterations in feeding intensity and links between spawning and feeding have never been examined in snoek. Dudley (1987) undertook a study on diel feeding periodicity, but his results are questionable as sample sizes were very small, and no continuous sampling was undertaken. It was with these unexplored topics in mind that the present study was conceived.

AIMS OF THE PRESENT STUDY

This study is essentially an in-depth evaluation of the fluctuations in the diet and feeding intensity of snoek and an attempt to examine aspects of these subjects not covered by previous studies. It is also an examination of methodology in diet studies, reviewing the techniques required to achieve an accurate description of the diet of a predatory fish, as well as the temporal scales at which dietary variation occurs. By undertaking such analyses, it is hoped to discover more about the plasticity of snoek feeding habits in relation to the variability of their prey resources, and also to provide information on the sample size and sampling frequency required to accurately describe future diets of this important predator.

Following from this background review, **Chapter 2** deals with precision in diet studies. The aim of this chapter is essentially to discover the optimum sample size needed to minimise sampling error when describing the diet of a predatory fish at the event scale. The key question was: what is the minimum sample size required to accurately describe the diet of snoek on any given day? It can be confidently stated that the error of a sample is reduced with increasing sample size, but practical considerations prevent sample collection from exceeding certain limits. Using

several analytical techniques, it is hoped that the results will allow the prediction of the degree of accuracy associated with a range of sample sizes. The design of a diet study can, at its simplest level, look at the presence or diversity of species in the diet. At a more complex level, the proportions of each prey type can be analysed, which is necessary for constructing ecosystem models. The analysis in this chapter will provide some guidelines on calculating the sample sizes appropriate for describing the diet of snoek in the Benguela ecosystem.

Chapter 3 deals with temporal variation in diet in a fixed area, at a seasonal scale. Samples collected inshore off the southwest coast in Region 3 (Fig. 1.1), were examined over a four-year period, grouped seasonally. The aim was to discover whether the seasonal migration patterns and thus availability of prey species, in particular pilchard and anchovy, are reflected in the diet of snoek in this region. Established theories on the migration and spawning of these species would lead one to predict that they would occur in greatest abundance in this area around winter and spring, and would thus occur more frequently in the diet during this period. If the more recent studies predicting winter spawning in anchovy were correct, however, it would mean a near-continual availability of both species in the area, with peak abundance in winter. In addition, it has been found that the distribution of anchovy is more widespread than previously thought and that, in years of high abundance, their range extends well round the Peninsula to the west during spawning (Roel *et al.*, 1994). Part of this chapter was dedicated to testing whether Crawford's assumption that snoek feed on anchovy for a fixed period during the year, is accurate. If not, the results may indicate that anchovy are available all year round in this area, and the diet may simply vary with the varying abundance of prey species in the region. An analysis of the diet of fish offshore will be used for comparative purposes, however far fewer data exist for this region. Links between the proportions of prey in the diet and their relative abundance in the environment were also examined, using catch statistics of pilchard and anchovy in the area sampled. Selectivity by snoek for pilchard and anchovy was investigated to determine whether snoek diet could be used as an indicator of the abundance of these two species.

Chapter 4 is an analysis of the seasonal trends in feeding intensity, spawning and condition of snoek, using the same seasonal grouping as in Chapter 3. As spawning occurs in winter and spring, it is expected that gonadosomatic indices will be higher during these periods. In contrast, fat content and condition are expected to be lower during spawning than during the rest of the year, due to the high energetic costs involved in gamete production. Seasonal trends in feeding behaviour were examined by plotting consumption indices or 'stomach fullness', as well as the percentage of stomachs containing food in each season. The link between feeding and spawning was investigated in order to determine whether snoek conformed to a 'ramper' (characterised by an intense period of feeding before and during spawning) or 'rester' pattern (cessation of feeding during spawning periods), as defined by Link and Burnett (2001). Comparisons between male and female fat, condition and feeding intensity were made, to investigate the relative costs of spawning. Griffiths' theory, mentioned earlier, suggests that female snoek are serial spawners that move inshore to feed on high-energy clupeoids between spawning bouts (Griffiths, 2002). If so, one would expect to find a higher percentage of females in the inshore samples, coupled with a diet dominated by clupeoid fish during the spawning season. Female feeding migrations were also linked to relative prey availability and to spawning and the energetic costs of reproduction.

Chapter 5 deals with variation in the diet over short time periods. Two time scales are investigated: within-season variation, and diurnal variation. Samples were collected weekly for six weeks over a small area around the Cape Peninsula, to negate the possible effects of regional variation. The first aim was to detect the degree to which the diet varied over this six-week period, within a fixed location. This may indicate how often sampling is required in order to provide an accurate measure of the diet, and describe the effects on sampling of short-term temporal variation. The diurnal variation in diet was examined using samples trawled offshore during a research cruise. The samples used were all obtained within a one nautical mile range of each other, and sampling took place at 6 hr intervals, morning, noon and evening. Due to the close spatial and temporal proximity of the samples, the fish caught could provide a good measure of diel feeding periodicity in snoek. Secondary aims were to examine whether there

were shifts in the diet over such short time intervals and where in the water column the fish were feeding (based on the freshness of prey items, where the snoek were caught, and the prey types consumed) and at what times of the diurnal cycle. These data were also used to make inferences about snoek feeding intensity during spawning, as sampling took place on the spawning grounds during winter. Differences in diel patterns of feeding intensity of male and female snoek were examined separately and compared.

Chapter 6 summarises the results obtained and conclusions drawn from earlier sections, and examines future research options for snoek. It is anticipated that this study will provide some salient theoretical data, which may translate into practical advice on methodology in dietary analyses. In addition, it is hoped that the re-examination of snoek diet in close detail and at several temporal scales will add to the ever-growing pool of knowledge on species interactions and processes of the Benguela ecosystem. This may be useful in the construction of ecosystem models, using software tools such as ECOSIM or ECOPATH, for which information on the diet, feeding intensity and consumption rate of species is essential. This research should provide some of the data needed in the construction of models, or highlight where further work is required.

Chapter 2:

The influence of sample size on the precision of dietary analysis.

Chapter 2

INTRODUCTION

Sampling and statistics

Snoek, *Thyrsites atun*, is a member of the snake-mackerel family (*Gempylidae*) and is found throughout the cold temperate shelf waters of the southern hemisphere. It is regarded as one of the most important predators of pelagic schooling species in the southern Benguela Ecosystem (Crawford *et al.*, 1992; Griffiths, 2002; Chapter 1).

In the process of studying a fish species, population or sub-population, many forms of measurement can be employed. Examples include meristic measurements (e.g. fin ray counts), morphometric measurements (e.g. body proportions, size frequency), physiological attributes (e.g. condition, fat content) and measurements of ecological parameters such as diet and habitat preference. In a genetically homogenous population (stock), meristic and morphometic measurements are generally highly predictable and easily described by mathematical formulae, usually showing a low degree of variation around the sample mean. Physiological attributes generally produce a greater degree of variation, as a result of events such as spawning and migration, but also due to the species' responses to changing environmental factors (Iversen, 1992). The most highly variable measurements tend to be obtained from ecological data. Of these, diet and feeding behaviour are, without doubt, amongst the most prone to fluctuation. This is attributable to factors such as spatial and temporal patchiness of prey resources, which occur from diel to decadal scales (Iversen, 1992; Bogstad *et al.*, 1995; Ferry and Cailliet, 1996).

Because diet is such an inherently variable parameter, it is far more challenging to obtain the same degree of precision in its quantification that is seen with the measurement of less variable characteristics. Hence, special considerations are necessary in the design, implementation and data analysis of dietary samples. This chapter examines one of the factors that have a great impact on the precision of diet descriptions - sample size.

Our inferences as to the characteristics of a population are based on observations of a small group of animals, the sample, in that population. Elementary statistics advocate that in sampling, it is desirable that the statistical sampling mean, x, will be a sound estimate of the population mean, μ. In order to achieve this, the standard deviation, s, around the sample mean must be minimised (Eason *et al.*, 1980). The simplest way in which this can be done is to increase n, the sample size, as is shown in the equation for standard error:

$$SE = \frac{s^2}{\sqrt{n}} \qquad \text{.....equation} \quad 2.1$$

Since standard error is inversely proportional to the square root of sample size, as **n** increases, sampling error decreases. Probability curves (Figure 2.1) also show clearly that x approaches μ, as n increases:

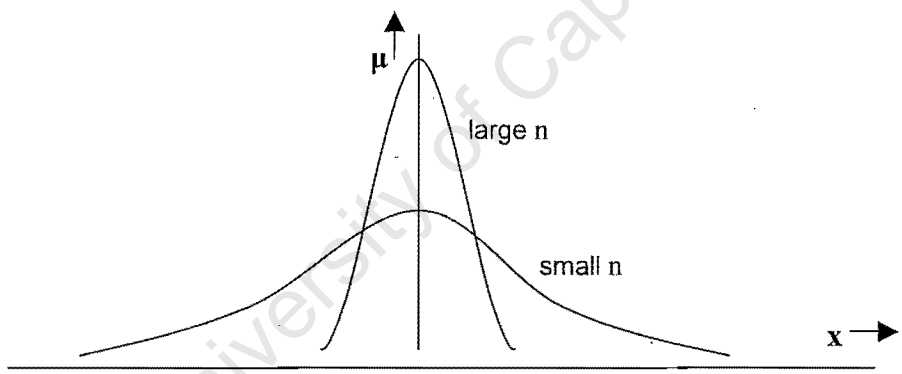


Figure 2.1: Probability curve showing how x approaches μ with increasing sample size (after Eason *et. al*, 1980)

Precision and types of diet studies

Accurate diet descriptions are necessary not only in order to understand the ecological role of a species, but also to enable comparisons between different locations, times, age classes, sexes and species (Ferry and Cailliet, 1996). In addition, predation and prey mortality are important components of multispecies models, and accurate descriptions of diet are necessary to assess species interactions such as predation and competition, and the ecosystem effects of overfishing (Hollowed *et al.*, 2000). Reliable and precise information on food consumption and

diet composition are vital in the construction of such models (Bogstad *et al.*, 1995). The basis for designing a sampling programme and choosing an appropriate sample size, is that the objectives of the study are clearly laid out and adequately catered for. It is self-evident that the sample size required for a diet study depends entirely on the purpose of that study and the degree of precision required (Duffy and Jackson, 1986). Examples of some types of diet study follow, with comments on the sample size requirements appropriate to each.

1. Food consumption studies: relating to daily ration, energy budgets, annual consumption rates, etc., do not require very numerous samples but rather, more frequent sampling in order to quantify patterns of diel feeding behaviour, feeding intensity, stomach fullness and so forth. Much work of this nature is, in fact, carried out under laboratory conditions and is not discussed in this study in terms of sample size.
2. Qualitative studies: These require simple presence and absence data on the prey types consumed by a predator, in order to build up a picture of the breadth of its feeding niche, and general diet diversity. Studies of this nature generally do not require huge sample sizes, and size requirements are easily calculated graphically using cumulative prey curves, as discussed later.
3. Quantitative studies: Here the exact proportions of each prey type are measured in relation to one another. Such data can be used to describe diet over various time scales (such as seasons, years or even decades) or within certain geographical areas, and this measure is the most important in building ecosystem models. Data of this type are vital in making comparisons, and often require much more substantial sample sizes to achieve accuracy (Duffy and Jackson, 1986).

The knowledge and affiliated testing and indication of the degree of precision with which diet is described is essential in order to make statistically confident inferences about populations. In an investigation into precision in diet sampling, Ferry and Calliet (1996) reviewed over 200 diet studies. Their work revealed that in most cases, no estimates of the precision of results or samples were included in the studies. In addition, no attempts were made to ascertain appropriate sample sizes for the purposes of the studies reviewed. A statistical extrapolation of

the data for these studies revealed that where no significant dietary differences were found by the researchers concerned, differences did in fact exist, but were undetected or overlooked due to small sample sizes. It was also found that many of these studies relied on indices for comparison, stating the presence of statistical differences, when no actual statistical analyses had been performed. Both of these problematic practices are serious design faults, and detract from the validity of the results obtained and conclusions drawn (Ferry and Cailliet, 1996).

Testing sample size

Several studies discuss the necessity for indicating the accuracy of results in diet analysis and advocate the testing of data, suggesting either an *a priori* review (when designing the experiment), or *a posteori* tests of the sample data obtained. Possibly the most common *a posteori* test employed in diet studies involves plotting a cumulative species curve, which is similar in nature to a common ecological function, the species-area curve. This is based on the principle that, as more stomachs are examined, new additional species will appear in the gut, but that this rate of accumulation will decline with increasing sample size. When plotted, the curve of species richness will thus reach an asymptote, as shown in Figure 2.2 (Hurturbia, 1972; Ferry and Cailliet, 1996). This asymptote is hereafter referred to as the 'diversity asymptote'. The mechanisms of calculating diversity range from a simple sum of species encountered, to the more complex calculation of diversity indices, but the principle remains the same. Authors such as Hurturbia (1972) calculate the diversity as an index, H, and with each new stomach added to the sample, diversity is recalculated.

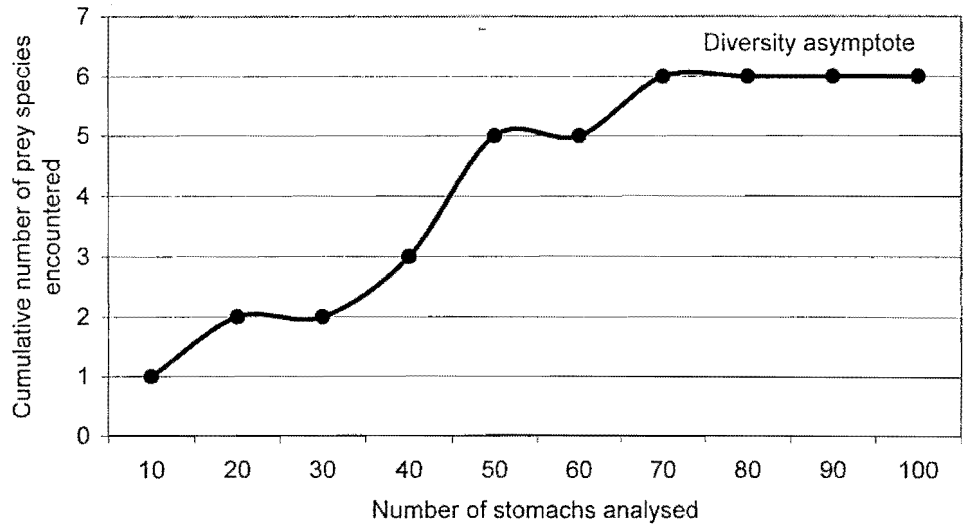


Figure 2.2: Cumulative prey curve showing number of prey types occurring with the number of stomachs analysed, plotted using data from a sample of snoek.

Cumulative diversity curves were first employed by Pielou (1966), and have been recommended and described by numerous authors since (*inter alia*: Elliot (1971), Hurturbia (1972), Baltz and Morejohn (1977), Cailliet (1977), Hoffman (1979), Calliet *et al.* (1986), Duffy and Jackson (1986), Griffiths (1997) and Cortẽs (1997), to name but a few). Ferry and Calliet (1996) go on to discuss that while cumulative prey curves are necessary for precision in diet studies, they are not enough on their own, and that the key to making powerful comparisons lies in attaining low levels of variation within samples. To this end, they advocate the use of power analyses (Appendix 2.1) that are best used *a proiri*, but can also be used *a posteori* to test the robustness of the conclusions drawn. These tests can take a number of forms. The ones employed by Ferry and Calliet (1996), involve setting the values of β (the probability of not rejecting a false null hypothesis) and α (the probability of falsely rejecting a true null hypothesis), at levels which will provide calculations of sample sizes needed to make statistically powerful comparisons.

AIMS

This study was conducted in order to ascertain suitable sample sizes for describing the diet of snoek, *Thyrsites atun*. Several previous studies have been conducted on the diet of snoek (De Jager, 1955; Nepgen, 1979a; Crawford and de Villiers, 1985; Crawford, 1989b; Dudley, 1987;

Griffiths, 2002, each of which have yielded varying and some since-refuted theories (see Chapter 1). The most comprehensive of these to date, Griffiths (2002), ascribes the shortcomings of the prior studies mainly to inadequate sample sizes. This is indeed evident in one example in particular, where the contents of six snoek stomachs were used to describe the diet of the species over an entire year (Nepgen, 1979; Crawford and de Villiers, 1985; Crawford, 1989). This is obviously an inadequate number to constitute a representative sample and make inferences about the population as a whole. The contention here is that the diet of snoek has not been adequately described until recently.

In addition to highlighting and reinforcing the problems associated with inadequate sampling, this study aims to determine the minimum number of stomachs required to provide a clear, precise description of the diet of snoek on any given day (sampling event). This excludes the pooling or resampling of data in order to bolster sample size and accuracy. The underlying question is: ' at the simplest practical level, how many snoek with stomachs containing food do we need to sample on one day in order to *accurately and precisely* describe their diet at that point in space and time?'

This study provides a review of detailed methods used in the analysis of sample size. The methods used and results obtained will describe how variance is minimised with increasing sample size, as pertains to

1. Diet diversity.
2. Exact prey proportions.
3. The standard error associated with prey proportions.

Methods and guidelines for sampling this species, and possibly other similar predatory species, are presented. Other techniques suited to the various purposes of diet studies, which are used to increase and test the precision of dietary data, are also presented and discussed (Appendix 2.1).

METHODS

Sample collection

The samples used in this analysis were drawn from a research programme conducted by Marine and Coastal Management between 1994 and 2001. Inshore and offshore samples were analysed separately, as diet has previously been demonstrated to vary with depth (Dudley, 1987; Griffiths, 2002)

Inshore samples

Line-caught samples were collected by handline fishing, using bait or lures, usually within about twenty-five kilometres of the coast, at depths ranging from 10 - 60 m. A six-week sampling programme was undertaken in False Bay in autumn 2001, with the aim of collecting 100 full snoek stomachs containing food per week. Success in obtaining this tally was dependent on the availability of snoek in the sampling area, as well as the proportion of fish in the samples with stomachs containing food. Samples were obtained one day per week, and were collected either by i) linefishing by research staff, or ii) collection of stomachs from fish vendors of commercially caught snoek. Data from four line-caught samples from the Marine and Coastal Management sampling programme were deemed large enough for this study and were included in the analysis, two obtained in 1996, and two in 1999. The number of stomachs containing food in each sample ranged from 60 to 115, with a mean of 89 (± 21.7).

Stomachs were removed from the fish and frozen immediately in order to prevent post-mortem digestion. Limited biological data were recorded for the fish, namely sex and fork length (to the nearest millimetre). Samples were thawed in the laboratory and stomach contents analysed wet, the assumption being the moisture content was the same as in a fresh sample.

Offshore samples

Large samples of snoek obtained on demersal research trawls were selected from the Marine and Coastal Management database. Ten samples , each comprising 60 or more stomachs containing food, were drawn from data obtained in the winter months of 1998 and 2000. Sample

number ranged from 61- 115 stomachs containing food, with a mean of 92 (± 19.1). These fish were trawled on the FRV Algoa on the seabed at depths ranging from 160 - 250 m. A German High-Lift trawl with a four-seam 180 ft net (110 mm mesh) was used. Sampling locations for the inshore and offshore data sets are plotted on Figure 2.3. Offshore stomachs were dissected at sea, immediately after the fish were caught.

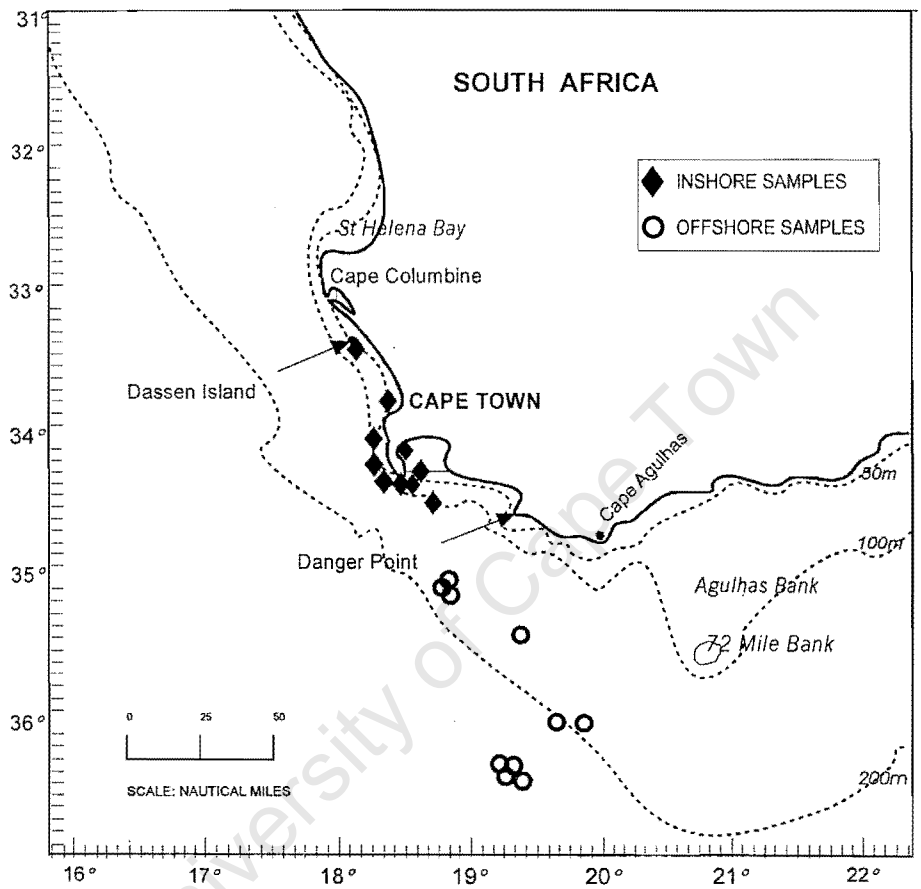


Figure 2.3: Map showing the South Western coast of South Africa indicating the locations of inshore and offshore samples.

Analysis

Prey items were identified to the lowest possible taxon and weighed wet to the nearest 0.1 g. Bait (in line-caught fish stomachs) and net-consumed items (in trawled fish stomachs) were generally easy to recognise and were discarded. The mass values for each prey type were summed and expressed as a percentage of the total prey mass. Unidentified prey were grouped discreetly and combined with those prey items contributing less than 5% to the diet to form the group "other". Diet was then plotted as percentage mass proportions in a stacked bar chart, with inshore and offshore diet plotted separately.

Each of the 20 samples was divided into cumulative 10-stomach classes. In other words, the first class or sample size was 10 stomachs, the second was 10 + 10 =20 stomachs, the third was 20+10 = 30, and so on. The analytical methods undertaken were done in terms of these classes, in order to test for increasing accuracy with increasing sample or class size.

Cumulative prey diversity

Cumulative prey diversity curves were plotted for all samples, where the number of new species appearing in the diet was plotted against the cumulative number of stomachs analysed. As previously mentioned, as the number of stomachs examined increases, so the number of new or unique prey types appearing declines, until eventually an asymptote is reached. This is described mathematically as:

$$S_n = f(n) \qquad \text{.....equation 2.2}$$

where S is the number of prey types found for (n) stomachs examined (Ferry and Calliet, 1996). These cumulative prey curves, an example of which is shown in Figure 2.2, were combined into a table (Table 2.2) where the point at which asymptote was reached is marked. The median, range, mean and standard deviation for this point were also calculated (using only samples where the asymptote was reached), the range and standard deviation providing measures of the variation in the point at which the asymptote was reached. This technique is only suitable to describe the precision of presence and absence data regarding prey diversity. A further investigation into the precision of prey proportions as described by various sample sizes, was thus undertaken.

Cumulative prey percentages

For each cumulative class of ten stomachs, the proportions of each prey type were calculated, as shown in Figure 2.4. As with the cumulative diversity curves, an asymptote, or stabilisation of the relative proportions of prey, occurs as the sample size increases.

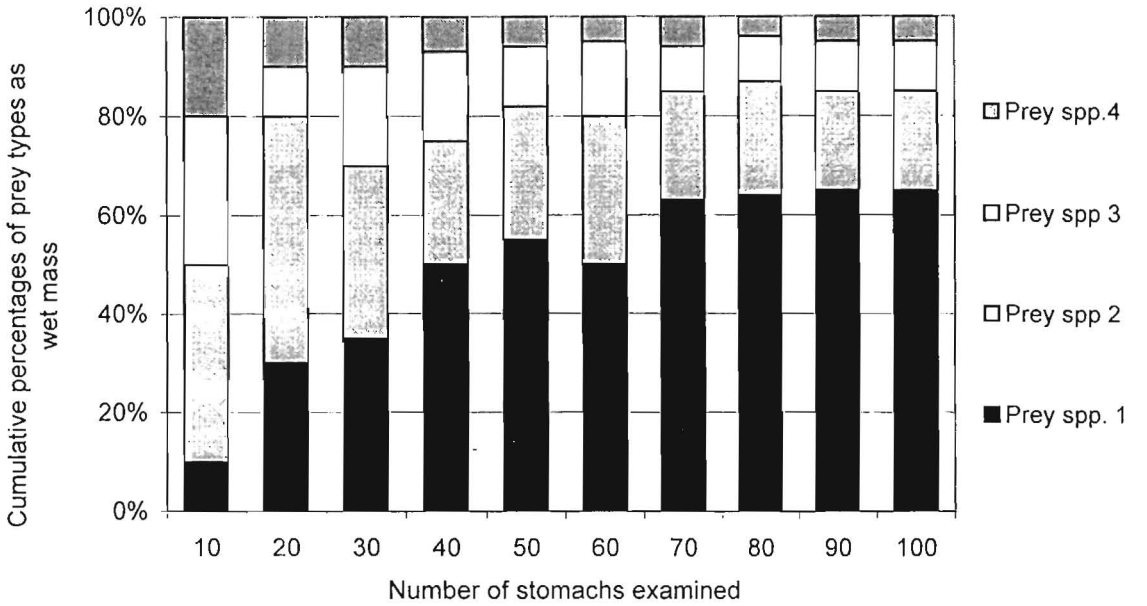


Figure 2.4: Example illustrating cumulative percentages for four prey types for a sample of 100 snoek stomachs.

In order to illustrate this stabilisation more effectively, the percentage difference of the main prey item was calculated between the classes. It must be emphasised here that 'main prey type' refers to the proportion of that prey species comprising the largest percentage by mass in the diet. This differs in nature from the phrase 'most important food', which has an ecological reference to the importance of prey in the overall diet of a species (Berg, 1979). The equation used was:

$$\mathbf{D}_{(n)} = \mathbf{P(i)}_{(n+10)} - \mathbf{P(i)}_{(n)} \qquad \text{.....equation 2.3}$$

Where **D** is the percentage difference between consecutive classes (n and n+10) , and **P** is the relative percentage of prey type **i** for the specified class. The mean values of **D** were then plotted for the in- and offshore samples, and standard deviation per class was calculated to indicate the degree of variation and how it decreases as class size increases. The mean asymptotic level of these curves was calculated as the sample number beyond which the difference of the main prey type between groups was less than 1%. In the cases where this difference was exceeded at the maximum sample number, the minimum percent difference reached was used (always <2%).

Standard error

The error associated with the cumulative percentage graphs mentioned was also calculated for each class for the main prey item in each sample. The equation used gives the error associated with a proportion:

$$\text{Standard Error} = \sqrt{\frac{p\,(1-p)}{(n-1)}} \qquad \text{.....equation 2.4}$$

Where **p** is the proportion of the main prey type, and **n** is the sample or class size. These error values were plotted on a scatter graph.

Calculated optimum sample sizes

The last method did not involve analysis of the samples, but rather the use of an equation cited by Duffy and Jackson (1986), for the calculation of appropriate sample sizes. This equation provides an estimate of the sample size required, **N**, so that the proportion, **p** of a prey species, (in this case the main prey item), has a 95% chance of being within a percentage **d** of the true value:

$$N = 4\,p \times (100 - p) / d^2 \qquad \text{.....equation 2.5}$$

Five values were chosen for **d**, namely 1%, 2.5%, 5%, 7.5% and 10%. The prey proportions (**p**) used were those for the main prey type for each sample, and the optimum sample sizes predicted by this equation are compared to the actual sample sizes taken (Table 2.2).

RESULTS

Diet

The diet of snoek for the 20 samples used in his aspect of the study is summarised in Figure 2.5. Inshore diet (Figure 2.5 a)) was dominated by anchovy (*Engraulis encrasicolus*), pilchard (*Sardinops sagax*), redeye round herring (*Etrumeus whiteheadi*), horse mackerel (*Trachurus trachurus. capensis*) and, in one of the samples, by the mantis shrimp (*Pterygosquilla armata capensis*).

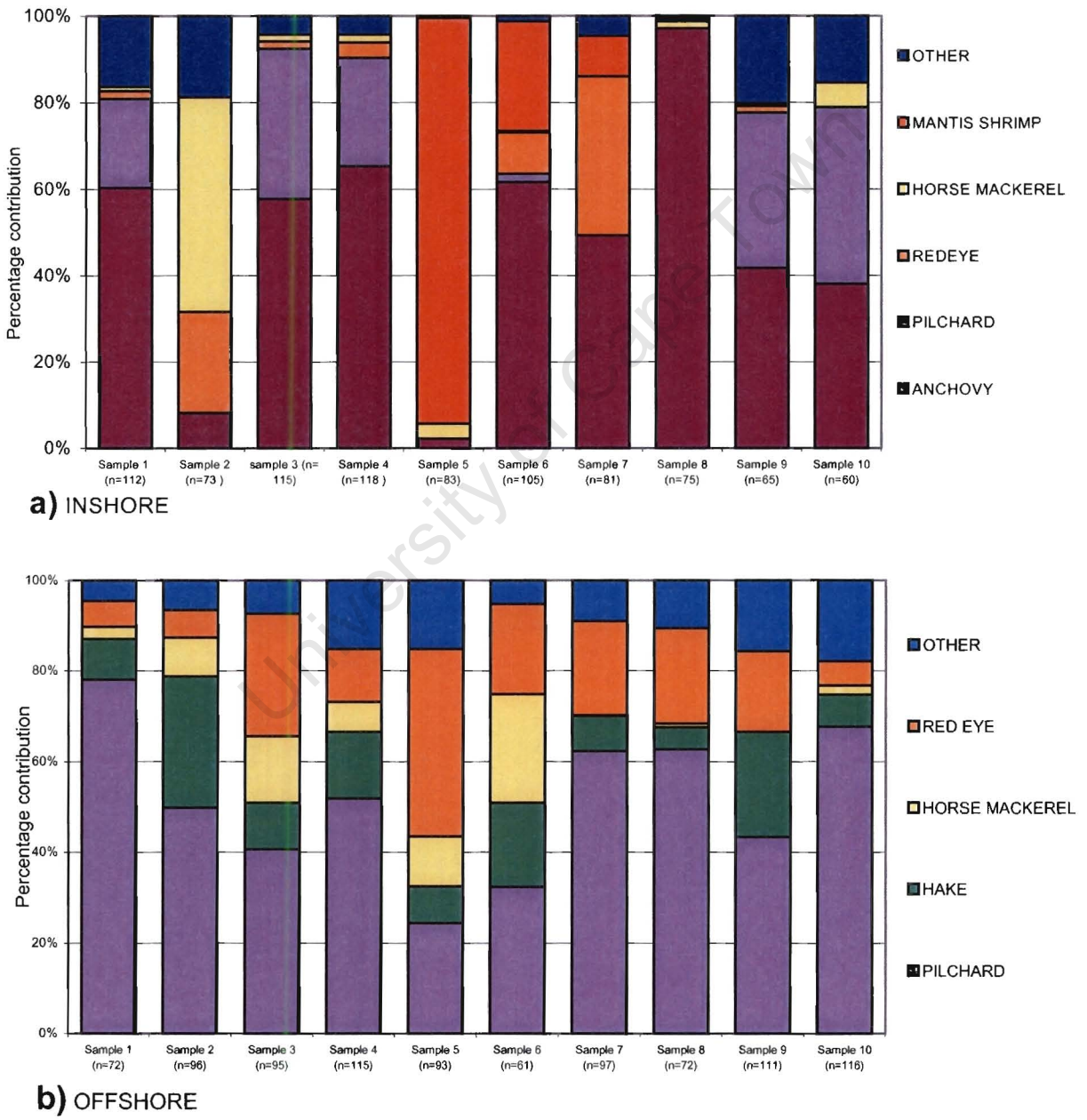


Figure 2.5: Proportional contributions as percentage wet weight of prey species for a) the ten inshore and b) the ten offshore samples. Sample sizes (i.e. stomachs containing food) for the data sets are also are indicated.

The offshore diet (Figure 2.5 b)) was dominated by pilchard and hake (*Merluccius spp.*), followed by horse mackerel and redeye. These spatial differences in diet are consistent with the distribution patterns of the prey species concerned, particularly regarding anchovy, which tend to occur closer inshore, and hake, usually found further offshore (Griffiths, 2002). A superficial examination of these graphs suggests that the inshore diet is more variable, with regard to both the species and proportions of the main prey types.

Cumulative prey diversity

Table 2.1 demonstrates how the diversity asymptote is reached with the increase in the number of stomachs examined per sample. The table clearly highlights the variability in the sample numbers required to reach maximum prey diversity totals. The stomachs in inshore samples contained a mean of 6.4 (± 0.84) prey species per sample, and those in offshore samples, a mean of 7.3 (± 1.33) species per sample. Data for the two sets of samples approximated normality, and thus a parametric test was performed. An ANOVA comparing the two sets revealed a near-significant difference in prey diversity per sample between on and offshore samples ($p = 0.054$; $F = 4.89$). The median level at which the diversity asymptote was reached was 30 stomachs (range: 10-70 stomachs) for inshore and 60 stomachs (range: 20-80 stomachs) for offshore samples. The mean values were 38.6 and 53.7 stomachs examined for the inshore ($n = 7$) and offshore ($n = 8$) samples respectively. Circled numbers on Table 2.1 show samples where the diversity asymptote was reached very late in the sample analysis, or was not reached at all. These samples were not included in the calculation of the mean and median asymptote values.

On examination of the diet graphs (Figures 2.5 a) and b)), prey diversity appears higher for the inshore samples, whereas overall diversity was actually higher in the offshore samples. This anomaly was caused by the presence of more 'rare' prey types in the offshore diet, where a total of 17 species were encountered in all 10 samples. The inshore diet contained fewer species overall (12), but those which appeared in the diet did so in consistently large enough proportions to allow inclusion into the graphs. The higher median and mean diversity asymptote

values for the offshore samples can thus probably be explained by the higher prey diversity in these samples (i.e. more stomachs would have to be examined before all prey species were encountered, as more rare prey types were present).

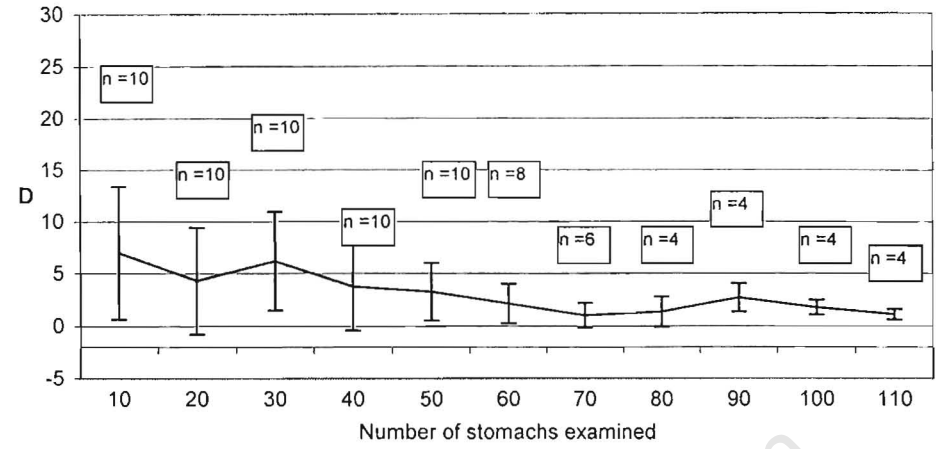
Table 2.1: The cumulative number of prey types are listed against sample sizes for the 10 inshore and 10 offshore data sets. The shaded blocks show the points at which maximum prey diversity was reached for each sample. The circled numbers indicate samples where the asymptote may not have been reached, shaded circles are where diversity continued to increase during the last 10 stomachs examined.

Stomachs examined	Number of prey species encountered		Shading indicates that the asymptote or maximum prey diversity has been reached for the sample.						
INSHORE	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6	Sample 7	Sample 8	Sample 9	Sample 10
1	1	1	1	1	1	1	1	1	2	4
2	3	2	1	2	1	1	1	1	5	5
3	3	3	1	2	1	3	1	1	5	5
4	3	4	2	3	1	3	1	1	5	5
5	3	5	3	3	1	3	2	1	5	5
10	3	6	3	3	2	4	3	1	6	5
20	5	6	3	4	3	5	4	1	6	7
30	5	6	4	5	6	7	5	3	7	7
40	5	6	5	5	6	7	5	3	7	7
50	5	6	5	5	7	7	5	3	7	7
60	6	6	5	5	7	7	5	3	8	7
70	6	6	5	6	7	7	5	5	(8)	
80	6		5	6	7	7	5	(6)		
90	6		5	6	7	7	5			
100	6		5	6		7				
110	6		(6)	6		7				
120										

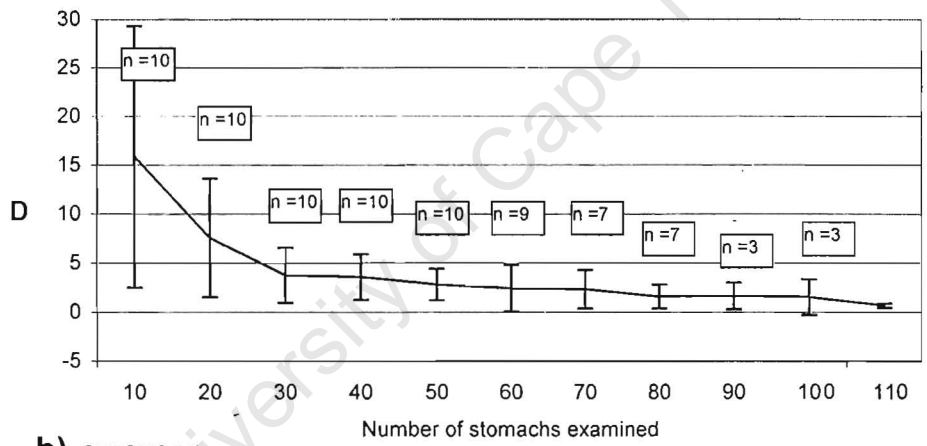
OFFSHORE	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6	Sample 7	Sample 8	Sample 9	Sample 10
1	1	1	1	1	1	2	1	1	1	1
2	2	2	1	1	2	2	3	2	2	1
3	2	2	2	3	2	3	3	3	4	2
4	3	2	2	5	2	3	4	3	5	2
5	3	2	2	6	3	4	4	3	5	3
10	4	3	4	6	4	5	5	3	6	6
20	5	5	6	6	5	6	5	4	6	7
30	6	6	6	6	5	6	5	5	6	7
40	6	6	6	7	6	6	6	5	6	7
50	6	6	6	7	6	6	6	5	8	7
60	6	7	9	8	6	6	6	6	8	8
70	6	7	9	8	6	6	6	(6)	8	8
80	6	7	9	9	7		6	(6)	8	8
90		7	9	9	(7)		6		8	8
100		7	9	9	(7)		6		8	8
110				9					9	8
120				9					(9)	8

Cumulative prey percentages

Figure 2.6 a) and b) show the mean percentage difference of the proportions of the main prey type with increasing sample size.



a): INSHORE



b): OFFSHORE

Figure 2.6: Plots showing the mean percentage difference, **D**, between ten-stomach classes, as per equation 2.3, for the main prey type for a) the ten inshore, and b) the ten offshore data sets. Vertical bars indicate the standard deviation on the mean difference for each class, and the number of samples appearing in each 10-stomach class is also indicated.

The mean sample size at which the asymptoytic level (**D** ≤ 1%, and < 2% in two cases) was reached was 74 (± 26.7) stomachs for inshore samples, and 79 (± 21.8) stomachs for the offshore samples. Notable, is the reduction in the standard deviation and hence degree of variation associated with the calculation of prey proportions as sample size increases. This was partly due to there being fewer very large samples.

Standard error

The relationship between standard error and sample size is illustrated in Figure 2.7.

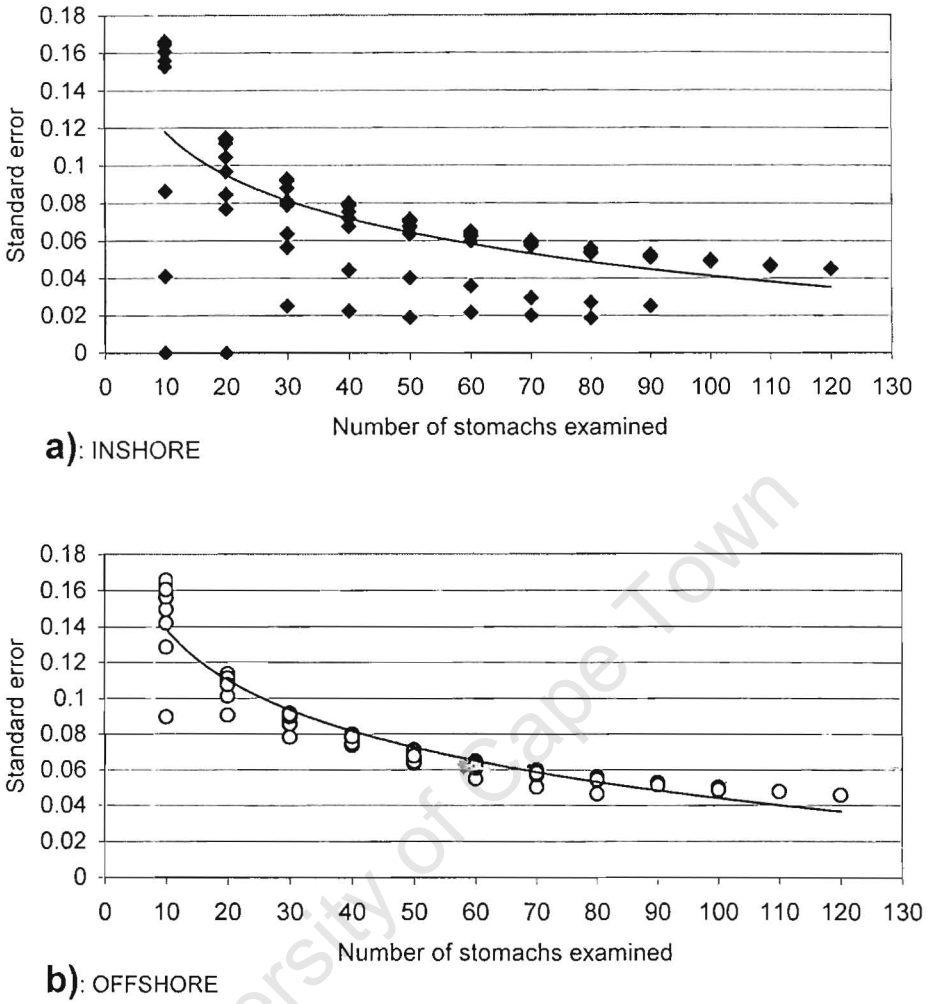


Figure 2.7: Scatter plots showing the reduction in standard error (as given by equation 2.4) associated with the proportion of the main prey type, as sample size increases for a) 10 inshore samples and, b) 10 offshore samples. Trend lines (least squares regression) indicate the decline in standard error with increasing sample size.

The calculation of the standard error is largely a function of sample size, but is also influenced by the proportion of the prey type in question. Standard error was reduced to a level of 0.06% after a mean of 65 (± 10.7) stomachs examined inshore, and mean of 66.7 (± 5) stomachs offshore. A standard error of 0.05 was reached after a mean of 85.7 (± 20.7) stomachs examined inshore, and 88.9 (± 12.7) stomachs examined offshore. Higher variation in standard error in the inshore samples (Figure 2.7 a)), can be partly explained by the higher variation in the proportions of the main prey types seen in this stratum (Fig. 2.5).

Calculated optimum sample sizes

Table 2.2 shows sample sizes calculated as per equation 2.5, for the proportion values of the main prey item for each sample. The calculated optimum sizes are compared to the actual sample sizes taken.

Table 2.2: Calculated optimum sample sizes, **N** for proportions **p** of a prey type, which will give a result that has a 95% probability of being within **d**% of the true value as given by equation 2.5, below. Calculated sample sizes are shown for the 20 data sets, for five values of 'd', showing the proportion of the main prey item for which 'N' was calculated. The actual sample sizes are shown in the right hand column. Shading indicates where the actual sample values matched or exceeded the 'required' values.

INSHORE Sample no:	Proportion, **p**, of main prey item for values of **d** =	Sample size **N**, recommended by the formula: $N = 4p \times (100 - p)/ d^2$					**Actual sample size**
		1%	**2.5%**	**5%**	**7.5%**	**10%**	
1	59.9	9608	1537	384	171	96	112
2	49.7	10000	1600	400	178	100	73
3	57.7	9763	1562	391	174	98	115
4	65.2	9076	1452	363	161	91	118
5	93.9	2291	367	92	41	23	83
6	61.6	9462	1514	378	168	95	105
7	49.3	9998	1600	400	178	100	81
8	97.1	1126	180	45	20	11	75
9	41.7	9724	1556	389	173	97	65
10	40.9	9669	1547	387	172	97	60
OFFSHORE							
Sample no:	**p**	**1%**	**2.5%**	**5%**	**7.5%**	**10%**	
1	78.1	6842	1095	274	122	68	72
2	49.8	10000	1600	400	178	100	96
3	40.7	9654	1545	386	172	97	95
4	51.8	9987	1598	399	178	100	115
5	41.4	9704	1553	388	173	97	93
6	32.3	8747	1399	350	155	87	61
7	62.3	9395	1503	376	167	94	97
8	62.7	9355	1497	374	166	94	72
9	43.4	9826	1572	393	175	98	111
10	67.7	8747	1399	350	155	87	116

The median optimum sample values were 96.5 and 94 stomachs containing food for the inshore and offshore samples respectively. These values relied heavily on the proportion of the prey type concerned. This means that data with proportion values close to 0% or 100% require much smaller samples to achieve the same accuracy than samples with a proportion approaching 50%.

DISCUSSION

Diet

The variations of prey proportions within the samples (Figures 2.5 a) and b)) are almost certainly attributable to the time span over which the samples were taken. This is especially so with the inshore samples, which were gathered over a period of six years. The larger fluctuations in the inshore samples, as compared with the offshore samples, are also possibly a result of seasonal changes in diet over the region sampled. Whereas the offshore samples were all trawled in winter, the inshore samples were taken in spring, summer and autumn. Prey resources, for example, pilchard and anchovy, are known to fluctuate seasonally in this region because of their spawning and recruitment migrations (Roel *et al.*, 1994). This may have contributed to the variation evident in Figure 2.5a). Week-to-week variation has also been shown to be high, in the inshore samples mentioned (Chapter 5). Aside from the difference in the within-sample variation between the in- and offshore data sets, the most notable difference is the absence of anchovy and the presence of hake in the offshore diet. This, as mentioned, is consistent with the distributions of these prey species.

Cumulative prey diversity

As can be seen in Table 2.1, in most of the samples, (90%), the diversity asymptote was reached well before all the stomachs had been examined. This indicates that the majority of these samples were large enough to accurately describe diet diversity in snoek. The mean sample size at which the diversity asymptote was reached was 38.6 stomachs for the inshore samples, and 53.7 stomachs for the offshore samples, the difference owing to the difference in diversity between in- and offshore diets. The median values of the diversity asymptote were 30 (range: 10-70) stomachs for inshore and 60 (range: 20-80) stomachs for offshore samples. This suggests at least 60 stomachs must be sampled in order to describe the total diversity or niche breadth of snoek in South African waters at the event scale. Niche breadth over larger spatial and temporal scales would require that sufficient samples were taken over time and across the distribution area of the species (see Chapter 5).

Cumulative prey percentages

As expected, a reduction in the percentage difference of the main prey type between successive classes was observed as sample size increased. There is a difference in variation between the inshore and offshore data sets, with the inshore set showing slightly higher standard deviations overall. This could be attributed to the higher variation in the proportions of the main prey items in the inshore diet, or to differences in the diversity of the two diets. Overall, the mean point at which the difference between successive classes was less than two percent occurred at 74 (± 26.7) stomachs containing food inshore, and 79 (± 21.8) stomachs offshore, for this species.

Standard error

The error graphs clearly show a reduction in sampling error with increasing sample size (Figure 2.7). Again, there is more variability in the inshore data set. As mentioned, this is because the prey proportions varied more overall, but also fluctuated between 10-stomach classes within samples. A standard error of 0.05 was reached in all but two samples, at a mean sample size of 85.7 (±20.7) stomachs inshore, and 88.9 (± 12.7) stomachs offshore.

Calculated optimum sample sizes

It is evident that as the value of 'd' decreases, the calculated sample sizes can become unreasonably large. The median optimal sample sizes recommended (for d = 10%) were 96.5 stomachs containing food for inshore samples and 94 stomachs for offshore samples. The actual sample sizes used matched or exceeded the calculated values with a value of d = 10%, in 55% of the samples. Southwood (1988) notes that a standard error that falls within 10% of the mean is perfectly acceptable, suggesting that most of these samples were of an adequate size to make inferences about a population. This technique highlights the role that the actual prey proportion plays in the selection of a sample size. A diet in which the main proportion tends toward 100%, requires far fewer samples to accurately describe it. This implies that a species that feeds almost exclusively on one food type, i.e. a specialist feeder, would require much lower sample sizes than a generalist feeder, where several significant prey proportions occur

simultaneously. This also applies to variable feeding behaviour within one species; for instance, a species may have a more specialised diet at certain times of the year, or in certain areas, depending on prey availability. The implication is that optimum sample size can change according to the behaviour and feeding regime of a species.

It must be stressed at this point that the sample sizes tested and discussed here only included the stomachs containing food in the samples. The proportion of stomachs containing food ranged from 20 to 95%, with a mean of 63%. This means that in order to reach these sample sizes, a considerably larger number of fish had to be sampled. This number was obviously dependent on the proportion of fish that had been feeding when sampling took place. Attaining or assessing sufficient sample sizes was relatively easy for the trawled samples, as the guts were dissected immediately after capture, allowing a running tally to be kept of the number of full stomachs obtained. The line-caught fish presented more of a problem, however, as the stomachs were frozen and only sampled later in the laboratory, giving no immediate idea of the proportion that contained food. To this end, a procedure of subsampling on site would have been appropriate, in order to roughly evaluate the percentage of fish that had been feeding. This would indicate the number of animals that would have had to be collected in order to attain the desired sample size, as full sampling on site was not possible. Familiarity with the feeding behaviour of the species in question is also useful in cases such as this, allowing researchers to take optimum advantage of feeding times and the seasonality of feeding intensity (Chapter 4), and thus obtain the maximum possible percentage of fish with full stomachs (Windell and Bowen, 1978).

Appendix 2.1 is an examination of some additional methods of minimising sources of variation in diet description. This includes descriptions of some of the techniques used by other authors to predict or test the accuracy of their data relative to the purpose of their studies. These techniques were not used in this study, as the emphasis was on determining optimal sample size, and thus only simple measures of precision were necessary. These techniques are worth

mentioning, but were deemed too time-consuming to attempt, in addition to the methods already used.

CONCLUSIONS

The issue of precision in diet studies is an often-overlooked one. Many authors advocate some form of testing and reporting of precision in studies. Baltz and Morejohn (1977) used cumulative prey curves and noted the limitations of their sample sizes. They note when the diversity asymptote was not reached, and go on to concede that their results do not adequately describe the niche breadth of the species concerned (Baltz and Morejohn, 1977). If testing reveals that the precision falls short, or that sample size is inadequate, an acknowledgement of these shortcomings by researchers is vital.

The use and display of cumulative prey curves is strongly recommended. It is felt, however, that this technique is not sufficient to test precision on its own, where exact prey proportions are being measured for comparative or other purposes. The use of additional forms of testing is recommended in this case. The plotting of percentage differences between successive classes was found to be a quick, efficient, and above all, simple method of testing accuracy. Power analyses such as used by Ferry and Cailliet (1996), and Cohen (1988) can be used *a priori* or *a posteori*, but are options that are more laborious (Appendix 2.1). Consideration of factors such as intra-haul correlation and the variation introduced by this must also be examined, and if possible, minimised in sample design (Chapter 5).

Despite statistical considerations, obtaining the desired sample size will always have logistical constraints. These are factors such as financial or time limitations, a restricted number of personnel, consideration for the rarity of a species (e.g. where the animal is at risk or protected), or difficulty in obtaining the sample animal. Such issues must be well considered, and a reasonable maximum limit must be set and accounted for by the researchers.

Taking into account the results of this study, the recommended sample sizes needed to describe snoek diet are as follows: For diversity description 55 (± 25) stomachs containing food should be sampled (depending on the niche breadth of the predator), as shown by cumulative diversity curves. For precise proportions, 75 – 80 (± 25) stomachs containing food should be examined, as drawn from cumulative percentage graphs. The standard error associated with the main prey proportion was reduced to 0.05 after 85 –90 (± 15) stomachs had been examined. From the median calculated optimum sample sizes, 90 – 100 (± 45) stomachs should be sampled to achieve a 95% probability of estimated prey proportions being within 10% of the true value of actual prey proportions. Thus, a 'safe range' for sample sizes would be between 50 and 100 stomachs containing food, depending on the purpose of the study in question. Actual prey proportions must be taken into account when deciding on a sample size, and subsampling could help to provide an idea of the prey proportions, as well as the percentage of fish in the sample with stomachs containing food. Higher diet diversity in the offshore samples generally meant that predicted sample sizes were larger and the variance of these totals was higher than in inshore samples. Thus, diet diversity should be considered when deciding on optimum sample sizes, as well as the aims of the study in question and the degree of accuracy required to achieve them.

As scientists, we aim for robust conclusions and assertions based on data. As Ferry and Cailliet (1996) state, " The conclusions one draws are only as good as the data on which they are based. There is no substitute for enough samples in reaching conclusions about the available data...". The use of predictive techniques or analysis of precision allows researchers greater power in the statements made and conclusions drawn. In doing this, our knowledge of the species we study is enhanced, and this in turn strengthens our understanding of ecology in general, widening our options for accurate, useful and effective applications of the data we gather.

APPENDIX 2.1: Summary of some additional techniques used to assess the precision of sampling techniques and predict required sample size.

Power analysis

In studies that necessitate comparisons of diet, Ferry and Cailliet (1996) recommend three equations that can be used to test the adequacy of sample size. These equations make use of set values for β and α. By convention, the values they used were β = 0.2 and α = 0.05 (after Zar, 1984). The results produced by these equations are estimations of the sample sizes needed to detect significant differences in diet, and are influenced by the actual differences in prey proportions between two or more samples. The differences in proportions are known as the 'effect size', and when making use of the equations, the authors suggest using the largest effect size in cases where there are more than two samples to choose from.

1. The first equation is used where indices (such as the Index of Relative Importance) are used to compare diet proportions. The equation states:

$$n = \frac{1570}{100 \times h^2} \qquad \text{.....equation 2.6}$$

where n is sample size, 1570 is the value described in Cohen's (1988) tables for the given values of β and α, and h is the arcsine-transformed effect size.

2. For samples that are compared using ANOVA or other parametric tests such as the t-test, the following equation is recommended:

$$n = \frac{(Z\beta + Z\alpha)^2 \times s^2}{d^2} \qquad \text{.....equation 2.7}$$

Where $Z\beta$ and $Z\alpha$ are the Z-values for β and α (if β = 0.2, Z = 0.85 and if α = 0.05, Z = 1.96); s^2 is the variance, and d^2 is the effect size.

3. The third test used, as suggested by Cohen (1988), tests the sample size needed to detect significant similarity or correlation, as opposed to significant difference:

$$n = \frac{1573 - 3}{100 \times z^2} + 3 \qquad \text{.....equation 2.8}$$

where 1573 is the value from Cohen's table for the values of β and α, and **z** is the Fischer-transformed value for the correlation coefficient, either Spearman's rank (r) or Kendall's Tau (T).

These equations are useful prediction tools as is equation 2.4 (used in this study), but they can also produce some highly unrealistic values for n. In such cases, the authors concede that the sample size needed is unattainable, and any diet difference that does exist is probably extremely small and would never be statistically detected (Ferry and Cailliet, 1996).

Resampling and bootstrapping

Tirasin and Jørgensen (1999) recommend a mathematical method of randomising samples in order to reduce variance and improve precision. This involves setting confidence limits on estimates of prey proportions, using resampling techniques.

Bootstrapping or resampling is a computer-intensive technique, first employed by Efron (1979). The aim is to estimate standard error and generate non-parametric confidence intervals for diet data sets. The bootstrap involves drawing samples at random from a data set, where each sample has an equal chance of being selected. The use of computers means that resamples can be replicated literally thousands of times over, with the variance decreasing as the number of replications is increased. The bootstrap method can only be used on one prey proportion at a time. This technique was proved to significantly reduce variation and the bias associated with intra-haul correlation and other non-random stratification in the data. The authors do note, however, that in order for the bootstrap to work, the original sample sizes used must be large

enough to be representative of the population in question. To quote: "No resampling method, regardless of the computer power, can replace a sound sampling procedure..." (Tirasin and Jørgensen, 1999).

Ferry and Cailliet (1996), also suggest a process of randomising the order of stomach content samples in order to reduce bias. They propose that the order of collection and thus sampling are often correlated to some other feature of sample design, and that in the procedure of plotting cumulative diversity curves, numerous randomisations should be undertaken. This entails calculating a mean number of new prey types for each gut, by randomising and resampling each sample, in other words, creating a large sample size of samples. This technique also allows calculation of the expected level variation in the point at which the asymptote is reached (Ferry and Cailliet, 1996).

Chapter 3:

Seasonal trends in the diet of snoek (*Thyrsites atun*)

Chapter 3

INTRODUCTION

Seasonal diet fluctuation and snoek diet

Two of the most influential factors in the feeding ecology of predatory fish are fluctuations in the biomass and types of prey species available. These variations imply that the diet of predators may change from day to day, seasonally, or over years, as the abundance of prey types fluctuates (Lagler *et al.*, 1977; Iversen, 1992). Seasonal changes in prey abundance and biomass are often a result of movements and changes in distribution linked to the prey species' own life cycle, (e.g. spawning migrations in fish, breeding aggregations in squid, periods of dormancy in invertebrates) (Keast, 1979).

Seasonal diet changes in predators are often very marked, particularly in contained freshwater systems such as lakes, where much work on the subject has been done (Wooton, 1990). They are often much harder to quantify in marine environments, because the oceanographic and climatic processes that in part influence the distribution of prey species, are highly variable and occur on a much wider scale here (Smale and Bruton, 1985; Wooton, 1990). In large-scale marine environments, the detection of seasonal fluctuations in prey abundance and hence diet, can be dampened by year-to-year and regional environmental variation (Wooton, 1990; Klages *et al.*, 1992). In such cases, it is often only possible to detect seasonal patterns in diet and prey abundance by concentrating the focus of the study on a limited region that represents only a small window area of the pertinent predator-prey relationships.

The area targeted in this study makes up a small part of the Southern Benguela ecosystem, an eastern-boundary current system, characterised by seasonal upwelling events (Shannon *et al.* 1992) (Region 3, Figure 1.1- Chapter 1). Snoek are top predators in this system, with a diet consisting principally of fish, 'supplemented' by crustaceans (Nepgen, 1982; Crawford and de Villiers, 1985). Previous studies (Chapter 1) have demonstrated that throughout the Benguela system, snoek prey extensively on pelagic schooling species, including anchovy (*Engraulis*

encrasicolus), pilchard (*Sardinops sagax*), horse mackerel (*Trachurus trachurus capensis*) and round herring (*Etrumeus whiteheadi*). The remainder of the diet consists of other fish, crustaceans such as euphausiids (e.g. *Euphausia lucens*), mantis shrimps (*Pterygosquilla armata capensis*), and cephalopods (mainly squid, e.g. *Loligo vulgaris reynaudii*). In the in the south-western region of the southern Benguela, snoek are regarded as one of the most important predator of anchovy, an important commercially harvested species (Nepgen, 1979 a and b; Crawford and de Villiers, 1985; Crawford, 1989). There is comprehensive knowledge of the overall diet of this species, and variations in prey proportions are apparent over large time scales (Nepgen, 1979; Crawford, 1987; Griffiths, 2002). However, nothing is known about possible seasonal trends in variation in diet, which was the purpose of this investigation. Identifying within-year fluctuations in the diet of a species is necessary in order to accurately describe the prey proportions in the annual diet and calculate yearly consumption rates of the various prey species. These parameters are vital in the construction of food-web models within an ecosystem (Hollowed *et al.*, 2000; Whipple *et al.*, 2000). There is reason to suspect that cyclic fluctuations may occur in the diet of snoek, as species identified as its main prey types undertake seasonal migrations and thus vary considerably in abundance from region to region, throughout the year, within the distribution range of the predator (Smale, 1992; Chapter 1).

Fluctuations in the prey species of snoek

On examination of the established migration patterns of the main prey types already identified in the snoek diet for inshore regions, it was possible to construct a reasonable estimate of their predicted annual movements in the selected area.

1. Anchovy (*Engraulis encrasicolus*): are found spawning around the Cape Peninsula, extending down onto the Agulhas Bank, in spring and summer. They cease spawning in autumn and one-year old fish are thought to move in an easterly direction along the south coast, while eggs and larvae are transported north to nursery grounds by the jet current. In times of high anchovy abundance, adults are also thought to move round the Cape Peninsula and north onto the West Coast after spawning (Barange *et al.*, 1999). Recruits begin to move southwards from nursery

grounds off the west coast in autumn, usually rounding the Cape Peninsula in late autumn, to arrive on the Agulhas Bank by spring. The population then extends onto the Central Agulhas Bank, or up the East coast in summer. These movement and distribution patterns suggest that their availability in the study area could be almost constant year-round, with spawning adults present in spring and summer, and recruits rounding the Peninsula in autumn and winter. The distribution of anchovy is highly temperature-dependant when spawning, and warm offshore water (> 20 °C) defines a clear boundary for the species. They tend to occur further inshore than other pelagic species when spawning. They could thus possibly be expected in greater abundance in the diet here during spawning, in spring and summer (Roel *et al.*, 1994, Shannon *et al.*, 1992).

2. Pilchard (*Sardinops sagax*): are thought to spawn year-round over the Agulhas Bank, where the core adult stock is found, as well as off the west coast (Barange *et al.*, 1999). Peak spawning occurs in late summer (February / March) and spring (September / October), associated with peaks in abundance on the Western Agulhas Bank. Recruits migrate along the same route as anchovy recruits, from the West Coast nursery grounds, round the Peninsula, onto the spawning grounds, although a second set are thought to mature on the south coast and move onto the Bank. Pilchard are generally found further offshore than anchovy, but are possibly more abundant than anchovy inshore at certain times of the year (Barange *et al.*, 1999). They have a wider but often much patchier distribution range, and seem to be less constrained by temperature. A portion of the population is thought to move inshore on the south and south-west coasts in summer, and might thus be predicted to occur in the diet of snoek in this region at this time of year. A lower availability in late autumn and winter may occur due to the start of an eastward migration of older pilchard onto and along the south and east coasts (the 'sardine-run'). Possible movements north, up the west coast may also occur at this time (Crawford *et al.*, 1989; Roel *et al.*, 1994; Barange *et al.*, 1999). Continuous spawning in this species may mean, however, that a constant stream of recruits moves around the Peninsula, implying a constant year-round supply of pilchard to the snoek in this region (Roel *et al.*, 1994).

As mentioned in Chapter 1, these two species undergo decadal-scale regime-shifts in dominance. Thus, the availability of each to snoek in this region will also depend upon which of the two is dominant at the time of the study. A trend of fluctuating abundance in these two prey types, with regime shifts, is seen in the diets of seabirds (particularly the Cape Gannet, *Morus capensis*), occurring off the west and southwest coasts. Since the mid-1980's, pilchard numbers have been on the rise, while anchovy numbers have shown pronounced fluctuations in recent years (Crawford, 1998; Barange *et al.*, 1999). After a peak in anchovy numbers in 1990 there were dramatic variations in the abundance of this species. Due to careful management, pilchard numbers have increased steadily since 1984, and throughout the period of this study, which will be discussed later. (Shannon *et al.*, 1992; Roel, 1994; Crawford, 1998; Barange *et al.*, 1999).

3. Other prey species: Some of the less dominant prey types found in snoek diet also undergo seasonal trends in availability from region to region.

Round herring have similar recruitment migrations to pilchard and anchovy. Spawning is concentrated further offshore in this species, on the outermost edges of the Agulhas Bank. They spawn year-round, with a peak from late winter to early summer (Armstrong and Thomas, 1989). Recruits and adults tend to occur inshore in late summer and autumn, meaning a potentially greater availability to snoek in Region 3 at this time of the year.

Mantis shrimps, (*Pterygosquilla armata capensis*), seem almost a 'supplement' to the diet and were observed by Crawford and de Villiers (1985) to dominate the diet on the west coast when pilchard and anchovy numbers were low. They occur in huge swarms near the surface of the water, in tightly packed 'balls'. They appear sporadically in the diet, and in cases when they do appear, they sometimes dominate the diet of most of the fish in a sample (Fig. 2.5, Chapter 2), suggesting that snoek take advantage of the swarming behaviour and feed solely on the crustaceans when they encounter them and nothing else is available. Mantis shrimps are found more commonly inshore on the west and south-west coasts during summer, but occur further

offshore and off the south coast during winter (Hopson, 1983). In other words, they are theoretically more accessible to snoek around the Peninsula in summer and spring.

Horse mackerel spawn offshore in cold waters (16 – 19 °C), over the Agulhas Bank from spring until autumn. The inshore diet of snoek in the study area comprises recruit-sized horse mackerel, rather than adults (Griffiths, pers. comm.*) and as recruitment occurs over the winter/spring period, abundance in the diet would possibly be higher at this time.

Hake (*Merluccius capensis* and *M. paradoxus*), which are sometimes found in the diet of snoek in inshore regions, are year-round serial spawners, with peak spawning in late winter/spring, and a smaller peak in summer. There is a size gradation by depth in these species, with juveniles being found closer inshore (Payne *et al.*, 1987; Punt *et al.* 1992). The spawning peak, in August, produces recruits which researchers believe congregate in a nursery area near the Orange River mouth (Figure 1.1), around January (mid-summer). It is postulated that they then move southwards, down the West Coast, and peak in seal diets around St. Helena Bay (Figure 3.1) in February – March (late summer). They continue to move south, and probably round the Peninsula in autumn. Year-old fish are then thought to move offshore, or further up the East Coast after August (late winter) (Leslie, pers. comm.*). The hake consumed inshore are more likely to be juvenile or near size at first spawning, as prey-size selection by snoek would definitely be a consideration where this species is concerned (Roel *et al.*, 1994). Their postulated distribution, would suggest that they would be most available to snoek around the Cape Peninsula in autumn and early winter.

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AIMS

The aim of this chapter was to investigate the seasonal variation in diet of snoek (*Thyrsites atun*), inshore around the Cape Peninsula on the south-western African coast. Seasonal trends were also examined for a limited number of offshore samples (taken in winter and spring, when snoek are available offshore), and the seasonality in the two regions was compared where possible. This study attempted to distinguish any relationship between the migration patterns of the main prey species, and their presence in diet of snoek. Crawford and de Villiers (1985) maintained that snoek only feed on anchovy for a fixed period during the year, which they related to the seasonal availability of the species. It was hoped that the results of this study would reveal whether this was, in fact, the case. Regional differences in the diet of snoek have been previously detected by Griffiths (2002), between two depth regimes, namely shallower than 50 m, and deeper than 150 m, on a wide geographic scale. While seasonal diet trends were the main focus, this study also aimed to test these regional differences in diet between on- and offshore sites more precisely over a small area.

This study aimed to detect possible seasonal diet trends, but also whether the relative prey proportions in snoek diet have fluctuated over the years with fluctuating pilchard and anchovy abundance. Correlations between the relative proportions of pilchard (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) in the commercial pelagic catch, and in the snoek diet were measured, to test the viability of using snoek diet as an indicator of the relative abundance of these two species in the environment. To this end, selectivity by snoek for pilchard and anchovy was also tested using catches as indicators of natural abundance. If the trends in diet and abundance are closely correlated and feeding was non-selective, snoek diet could be used as an indicator of the abundance and relative proportions of its most important prey species. Because of the commercial snoek fishery, stomach samples would be easier and more cost-effective to collect, than bird stomach samples, which necessitate costly sea-trips. If, however, snoek were found to actively select for one or other of the species, it would not be a feasible fine-scale indicator of relative abundance, as bias would be introduced in the estimates.

METHODS

Sample collection

Snoek were sampled along the South African coastline, which was divided into seven sampling sub regions (Figure 1.1, Chapter 1), from Port Nolloth to Mossel Bay. Sampling was conducted by Marine and Coastal Management from September 1994 - May 2001, producing an extensive database on snoek. The data used for seasonal dietary analyses in this chapter are a subset of this database, collected from September 1994 - January 1998, where sampling was continuous for all consecutive seasons.

The fish were collected in two ways: 'Inshore' samples (★, Figure 3.1) were collected by hand-line fishing, either by research staff or by commercial line-fisheries. Hooks were baited using cut or whole baitfish, usually pilchard (*Sardinops sagax*). Line-caught samples were generally fished at depths less than 60 m, by small fishing vessels operating within 25 km of the coast, and line-caught samples are thus referred to as 'inshore' samples hereafter.

'Offshore' samples (✕ on Figure 3.1) were gathered by trawling by the commercial demersal trawl fishery or on pelagic and demersal biomass research surveys. Trawled samples were usually caught at depths greater than 150 m, and thus occurred further offshore, generally between the 150 - 450 m isobaths. For the purposes of this study, all samples collected in this manner are referred to as 'offshore' samples. The specific trawl methods are described in detail by Griffiths (2002).

Inshore and offshore samples were analysed separately in some cases, as the sampling methods were gear-selective (hook and trawl-mesh size), making certain comparisons untenable. Previous studies also showed that diet varied considerably with depth (Griffiths, 2002)

Biological sampling of the fish involved measuring fork length to the nearest millimetre, and total mass to the nearest gram. The fish were then dissected and sexed. Gonads were removed and weighed to the nearest 0.1 g.

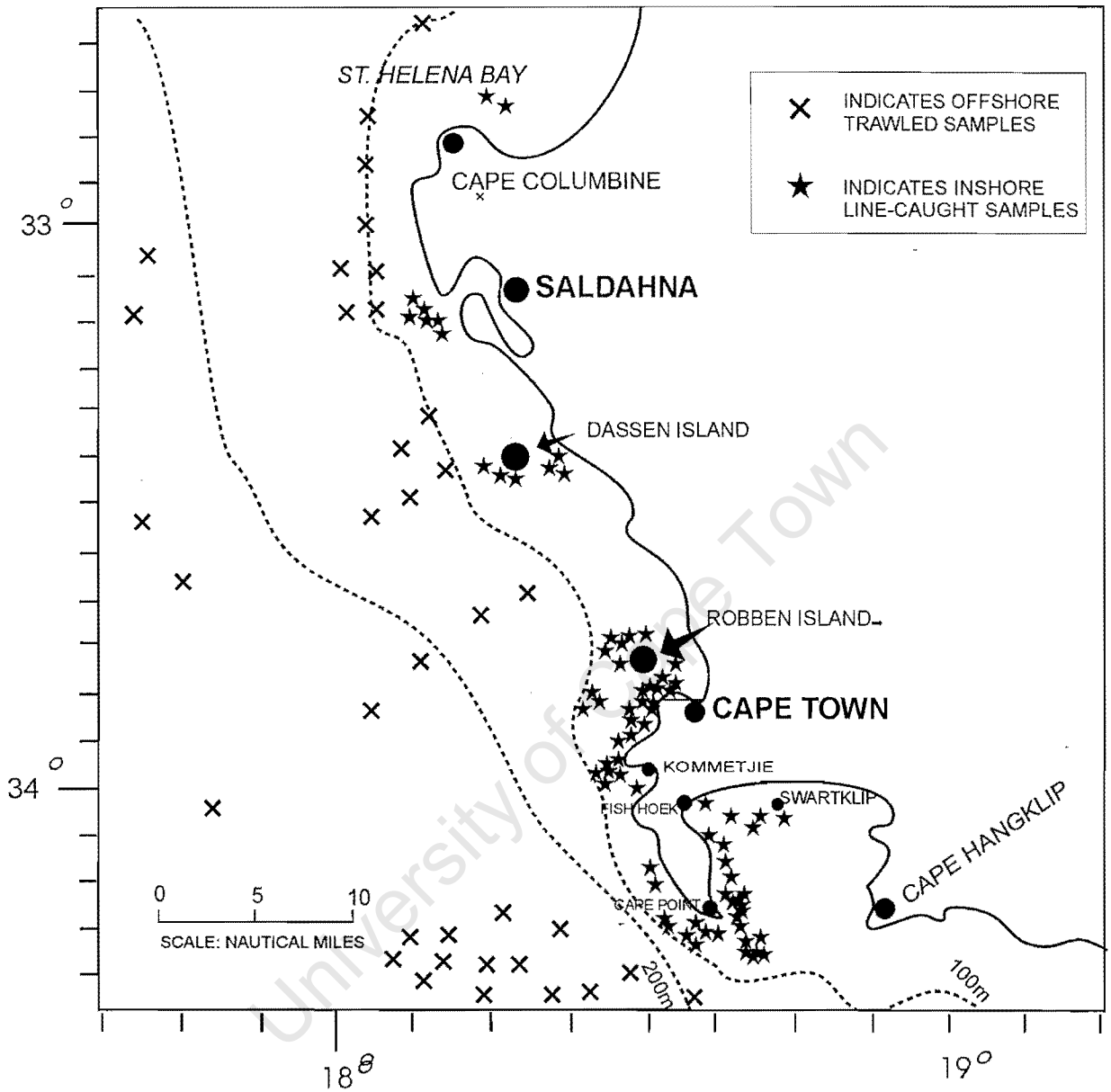


Figure 3.1: Map of the south-western coast of South Africa (detail of Region 3), showing sampling sites

In the case of research trawl samples, the stomachs were dissected fresh on board ship. Line caught and commercially trawled stomach samples were labelled and frozen, or stored in crushed ice, to be thawed and dissected in the laboratory later that day or the following day. Prey items were identified to the lowest possible taxon and weighed wet to the nearest 0.1 g. Bait (in line-caught stomachs) and net-consumed items (in trawled stomachs) were easily recognised and discarded.

Analysis

The year was divided into seasons as follows: autumn: March - May; winter: June – August; spring: September – November; summer: December - February (of the following year). The food choice of snoek is known to alter with fish size, as evidenced by the ontogenetic diet shifts found by Griffiths (2002). This meant that in stomach content analysis, only adult fish could be used, as sample sizes for juveniles were too small to analyse them as a separate group. Therefore in analysis, only fish with a fork length of greater than 700 mm were used. The size at 50% maturity for this species was calculated by Griffiths (2002) to be 730 mm, with a lower confidence interval (CI) of 700 mm and an upper CI of 752 mm. The lower CI was selected as a cut-off measurement for the analyses, to ensure maximum sample sizes and thus minimise sample variance (Chapter 2). The fish used in dietary analysis were only those with stomachs containing food.

Stomach content data could not be pooled across regions, due to possible regional differences in diet. Inshore and offshore samples were also examined separately for this reason; Griffiths (2002) described differences in the diet between fish feeding in deep and shallow waters. Small sample sizes precluded the use of all data except those from Region 3 (Figure 1.1), and even here, some of the sample sizes employed (Table 3.1), are far from the optimal sizes, discussed in Chapter 2. These inadequate sample sizes are circled in Table 3.1.

The mass values for each prey type were summed and expressed as a percentage of total prey mass. Unidentified prey were grouped discreetly and combined with those prey items contributing less than 5% to the diet to form the group "other". Diet was then plotted as percentage mass proportions in a stacked bar chart. Percent mass was considered a suitable measurement for diet proportions in this study as it is considered a more appropriate and direct measure where biomass-flows are important, e.g. in ecosystem modelling. The possibility of redundancy of variables in using compound indices as discussed by MacDonald and Green (1983) factored into this decision as well (Chapter 1).

Table 3.1: Synopsis of the sample sizes (number of stomachs containing food) used in summarising the diet inshore and offshore. Circles indicate where sample sizes may be inadequate for accurate diet description (see Chapter 2)

INSHORE	Spring	Summer	Autumn	Winter
1994	44	(27)		
1995	90	68	(38)	236
1996	83	81	(41)	305
1997	(20)		54	76
OFFSHORE				
1995				(30)
1996	154			148
1997				(21)

Prey proportions were subject to multivariate analysis using PRIMER® for Windows™, (release 5.0). To detect seasonal variation and possible grouping of similar prey proportions within seasons, a two-way nested ANOSIM was performed on the inshore data for Region 3. The offshore data did not include all of the seasons, as snoek are only available on the trawl grounds in winter and spring (Griffiths, 2002), and so could not be subjected to the same analysis. Regional diet differences were explored for Region 3, using matched seasons for the inshore and offshore samples. 'Matched seasons' refers to seasons and years where diet data existed for both in- and offshore regions simultaneously. This was done using a one-way ANOSIM. Graphic representations of the similarity between samples were produced by means of Bray-Curtis similarity matrices, from which multidimensional-scaling (MDS) plots and cluster analyses were drawn (Clarke and Warwick, 1994).

In order to understand the seasonal variation in dietary proportions, the relative abundance of the principle inshore prey items (pilchard and anchovy) was estimated using catch statistics from the purse-seine fishery (supplied by Marine and Coastal Management*). The catch tonnage was calculated as a rough index of natural abundance, per season for pilchard and anchovy, in the area in Region 3 where the inshore snoek stomachs were sampled (Figure 3.2).

* Purse-seine fishery catch reports (1994 – 1997), Marine and Coastal Management. Unpublished data

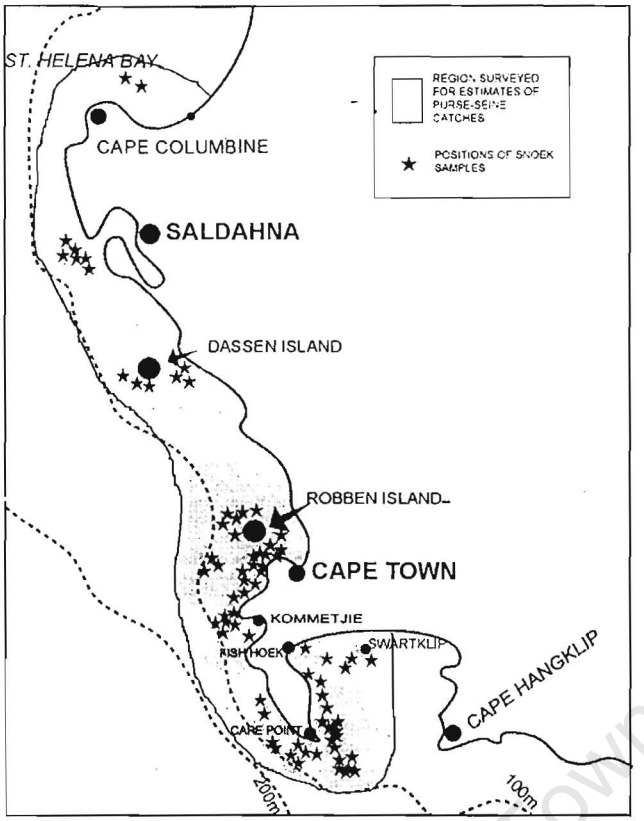


Figure 3.2: Map showing the area for which purse-seine catches were calculated from 1994-1997

Using these catch data, Pearson's product moment correlation coefficient was employed to test whether prey proportions in snoek diet and the relative proportions in the commercial catches showed any correlations. As catch statistics were used as an indicator of prey abundance, they were also used to test the selectivity by snoek for pilchard and anchovy. The test used was a modified version of the Shorigen Index, proposed by Berg (1979), where:

$$\text{Selectivity} = \log_{10} \frac{\%M_i \text{ in the ingested food}}{\%\ M_i \text{ in the potentially available food}} \quad \ldots\ldots\ldots \textit{equation 3.1}$$

Where % M_i is equal to the percent mass of the prey item in question (as opposed to the numerical percentage used by Berg (1979). Selectivity ranges from +∞ (preference) to - ∞ (avoidance), with 0 indicating random feeding. This index can be converted to the original Shorigen Index, using the formula:

$$K = 10^{sel} \quad \ldots\ldots\ldots\ldots \textit{equation 3.2}$$

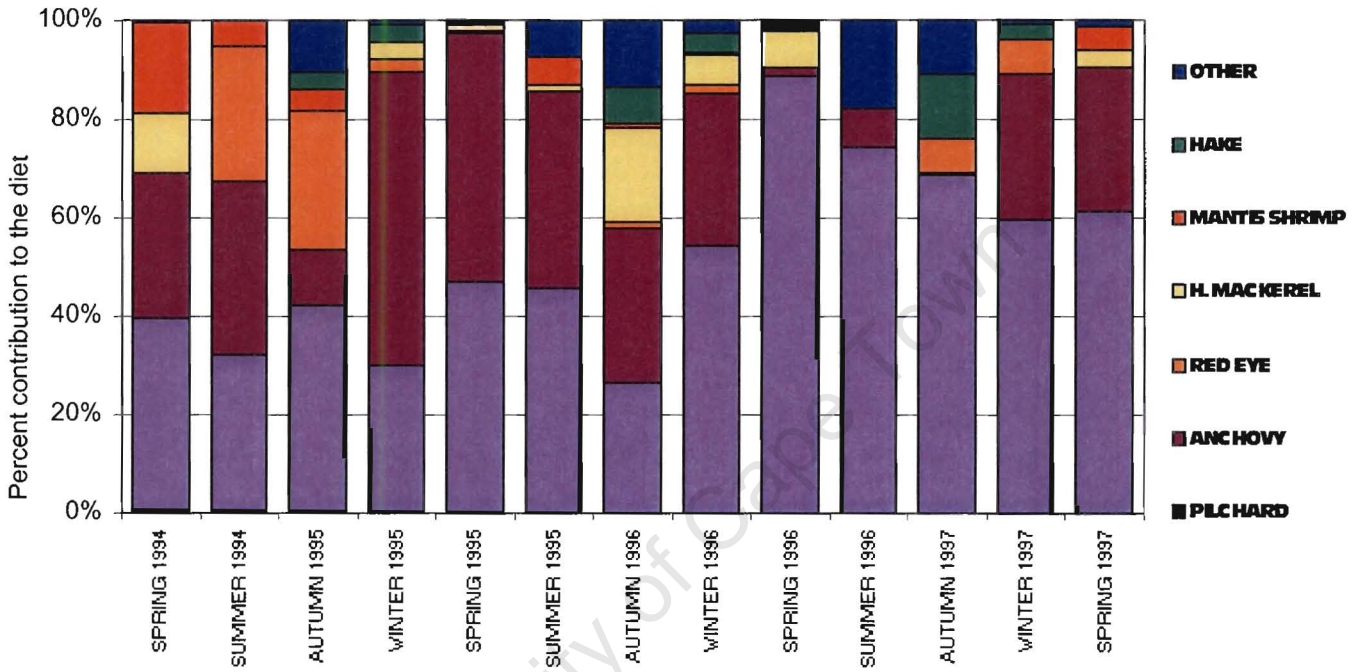
Where **K** indicates the degree of selectivity, with complete avoidance receiving a value of 0 (Berg, 1979; Smale and Bruton, 1985). This conversion was not considered necessary in the assessment of selectivity in snoek, as only two prey types were being compared.

RESULTS

Diet

Snoek were found to consume a wide diversity of species. These included 11 species of pelagic teleosts, 11 demersal teleosts, and one reef fish. Also found were eight crustacean, four cephalopod and one annelid species (Appendix 3.1). The diet as described by Griffiths (2002), based on samples taken over a wider area and a longer time-span, is even more diverse.

a)



b)

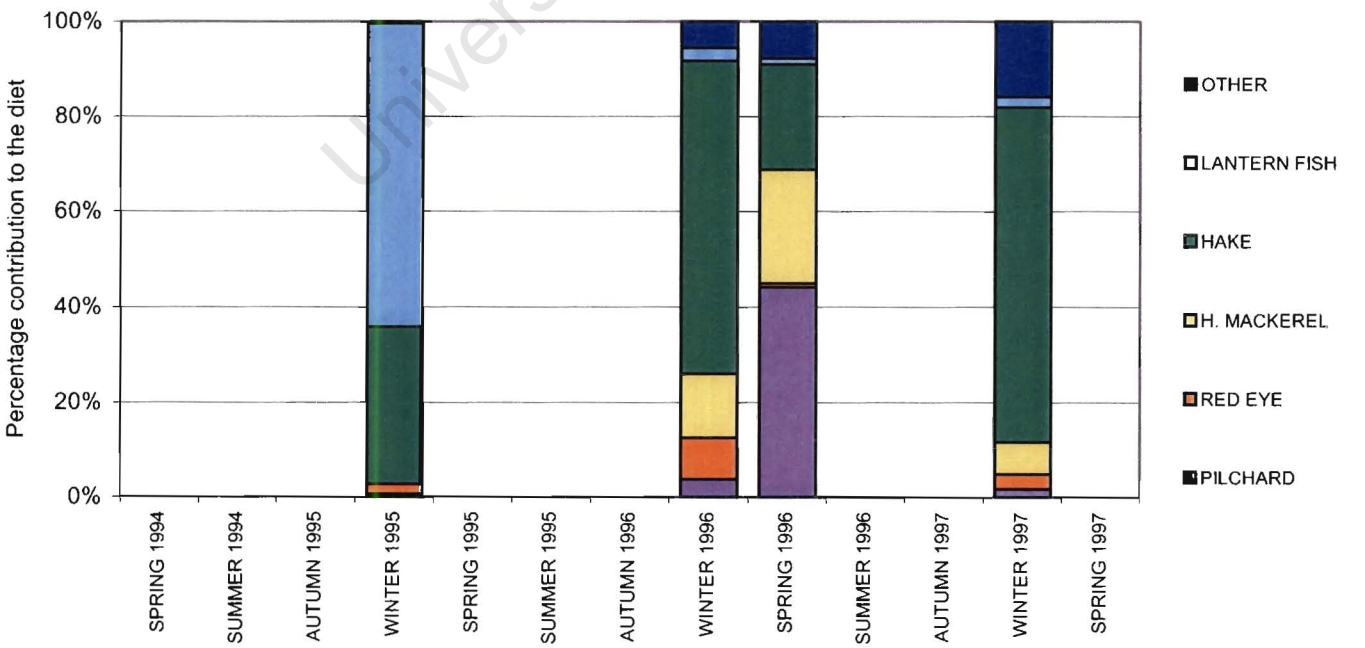


Figure 3.3: Seasonal contributions of prey types to the diets of snoek a) inshore and b) offshore in Region 3 (1994-1997).

The inshore diet in Region 3 was dominated by two pelagic species - pilchard (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) - which occurred in almost equal proportions in spring and summer 1994, as well as in winter, spring and summer 1995, and autumn 1996 (Figure 3.3 a)). Pilchard dominated the diet in autumn 1995 and from winter 1996 through to spring 1997. Anchovy were only dominant in winter 1995, and were almost absent from the diet in autumn 1995 and from spring 1996 to autumn 1997. Following these two species in dominance was another pelagic shoaling species, round herring (also called red eye) (*Etrumeus whiteheadi*), which was prominent in the diet in summer 1994 and autumn 1995, but appeared only in small amounts after this. Horse mackerel (*Trachurus trachurus capensis*) and mantis shrimp (*Pterygosquilla armata capensis*) appeared sporadically in small amounts over the period sampled. Juvenile hake (*Merluccius spp.*) also feature in the inshore diet, albeit rarely. Additional species occurring in very small quantities (< 5% mass), which make up the group 'other', are listed in Appendix 3.1.

The offshore diet in Region 3 was dominated overall by the two species of hake (*Merluccius capensis* and *M. paradoxis*) which are grouped together (Figure 3.3 b)). Hake dominated in winter 1996 and winter 1997. Pilchard and horse mackerel were also present in the offshore diet, particularly in spring 1996, while winter 1995 was dominated by lantern fish (*Lampanyctodes hectoris.*). The difference in species composition between the inshore and offshore diets is clear, and was corroborated by statistical testing.

Seasonal diet similarity

A two-way nested ANOSIM, which analysed the similarity of diets grouped seasonally, showed no significant relationship between season and similarity of diet composition (R=0.143; p=0.17 with 35 permutations and 999 data simulations)

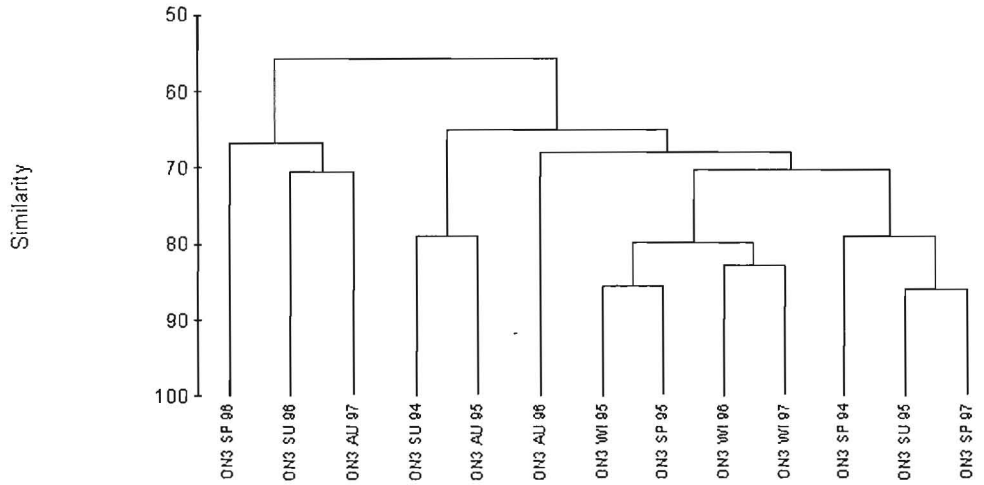


Figure 3.4 : Dendogram of the cluster analysis showing the percentage similarity between seasons for each year. The codes on this diagram are as follows: ON = inshore; SP = spring; SU = summer; AU = autumn; WI = winter; 3 = Region 3 and 96, 97, etc refer to the year.

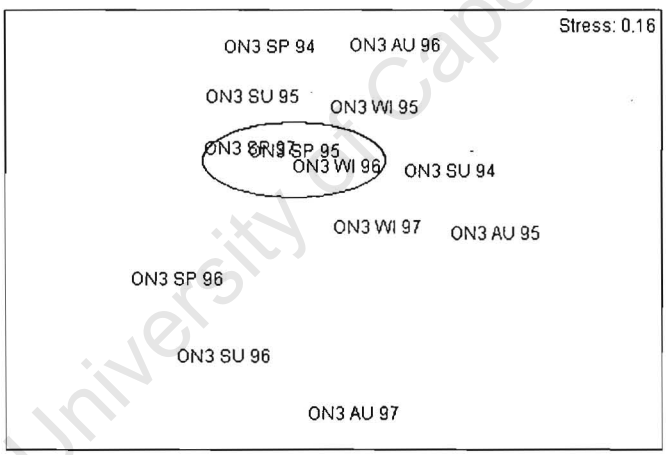


Figure 3.5: Multidimensional scaling plot of inshore diet for Region 3. The closeness of points on the plot indicates their similarity. The codes on this diagram are as follows: ON = inshore; SP = spring; SU = summer; AU = autumn; WI = winter; 3 = Region 3 and 96, 97, etc refer to the year.

Figures 3.4 and 3.5 are graphic representations of the Bray-Curtis similarity measure. Figure 3.4 is a cluster analysis of the inshore diet, which shows no clear seasonal grouping of the prey proportions. In the multidimensional scaling plot (Figure 3.5), the only samples which group slightly, are spring 1995, winter 1996 and spring 1997. The seasons to the left of the division correspond to periods of very low anchovy abundance, possibly explaining the grouping (Barange *et al.*, 1999). On examination of the bar graph, the prey proportions in these samples are very similar, which accounts for the grouping. On the MDS plot, the autumn measurements

seem to group out further away from the rest, indicating that autumn diet may be less similar to, or more variable than the diet during the rest of the year. The low stress value (0.16) for the MDS plot indicates that it is a good representation of the data (Clarke and Warwick, 1994).

Regional diet similarity

A one-way ANOSIM was performed, comparing diet data in- and offshore, where samples existed for both regions and seasons simultaneously. A significant difference between on and offshore sites was found (R=0.885; p=0.029 with 35 permutations and 999 data simulations)

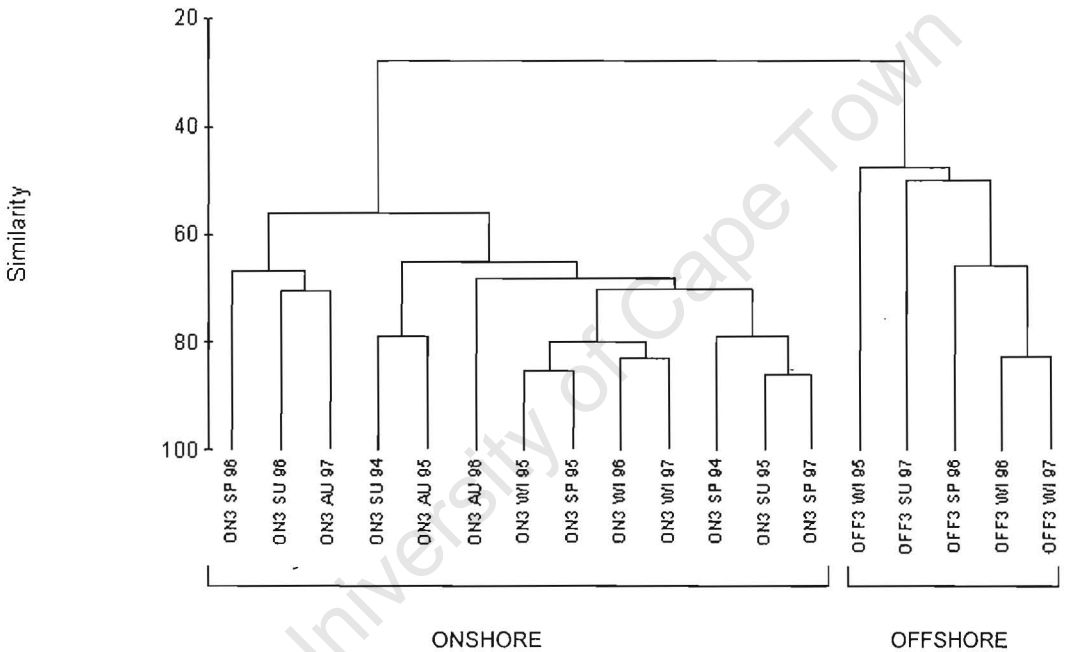


Figure 3.6: Dendogram of the cluster analysis showing the percentage diet similarity between regions (inshore and offshore). The codes on this diagram are as follows: ON = inshore; OFF = offshore; SP = spring; SU = summer; AU = autumn; WI = winter; 3 = Region 3 and 96, 97, etc refer to the year.

Figures 3.6 and 3.7 are graphic representations of the Bray – Curtis similarity measure between inshore and offshore samples. The regional groupings are clear in cluster analysis, where a similarity of less than 30% existed between the two groups, and the MDS plot, where the clear grouping of inshore samples is outlined. The very low stress level (0.08) of the MDS plot indicates the high accuracy of this representation of similarity (Clarke and Warwick, 1994). These results indicate that a clear distinction exists between the diets of snoek inshore and offshore.

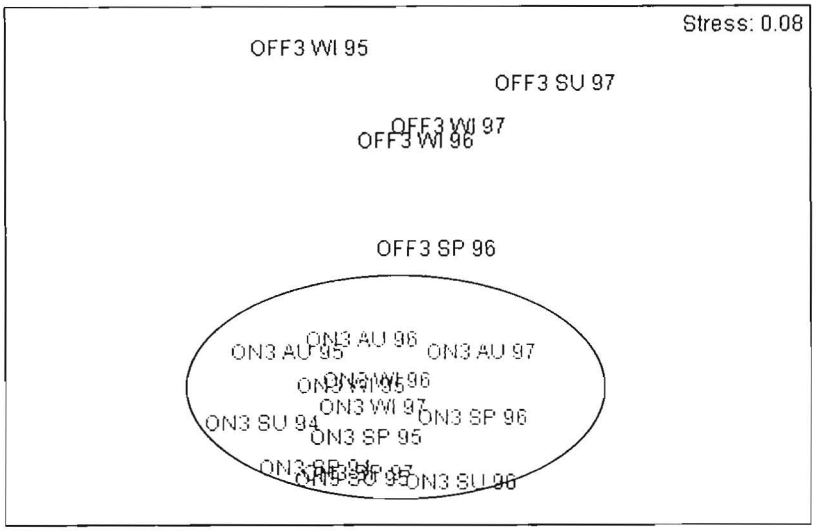


Figure 3.7: Multidimensional scaling plot showing similarities between inshore and offshore diet. The closeness of points on the plot indicates their similarity. The codes on this diagram are as follows: ON = inshore; OFF = offshore; SP = spring; SU = summer; AU = autumn; WI = winter; 3 = Region 3 and 96, 97, etc refer to the year.

Relative abundance of prey and selectivity by snoek

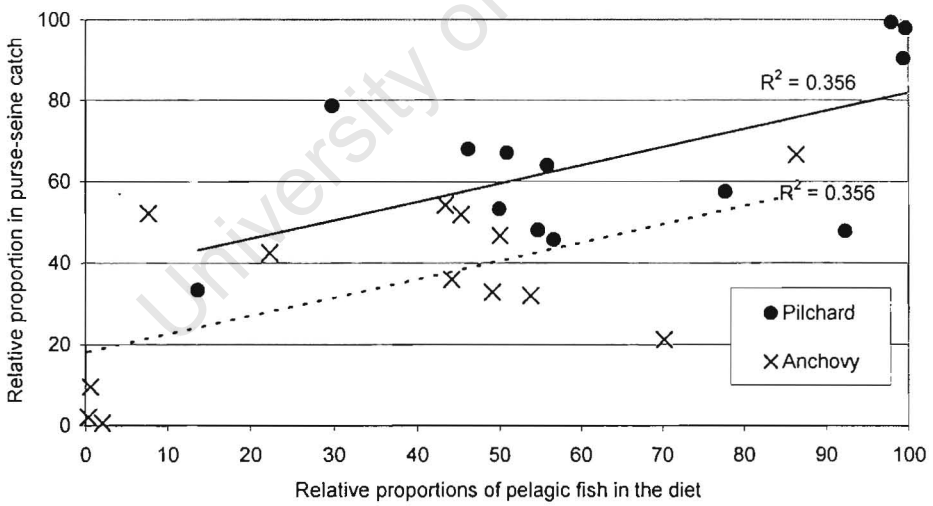


Figure 3.8: The relative proportions of pilchard and anchovy in the diet of snoek plotted against relative proportions in purse-seine catches, around the Cape Peninsula per season from 1994 to 1997.

A comparison of the proportions of these two species in the diet with the actual amounts caught by the fishery, showed a significant correlation (r = 0.6 for both prey species) (Figure 3.8).

The relative proportions of pilchard and anchovy in the snoek diet was a close match to their availability to fisheries in the same area (particularly from 1995 onwards) as evidenced by the correlation, and the trends are shown in Figure 3.9 a) and b). This mirror trend did not apply to the other species in purse seine catches (horse mackerel and round herring), possibly due to selective targeting of these species by the fishery.

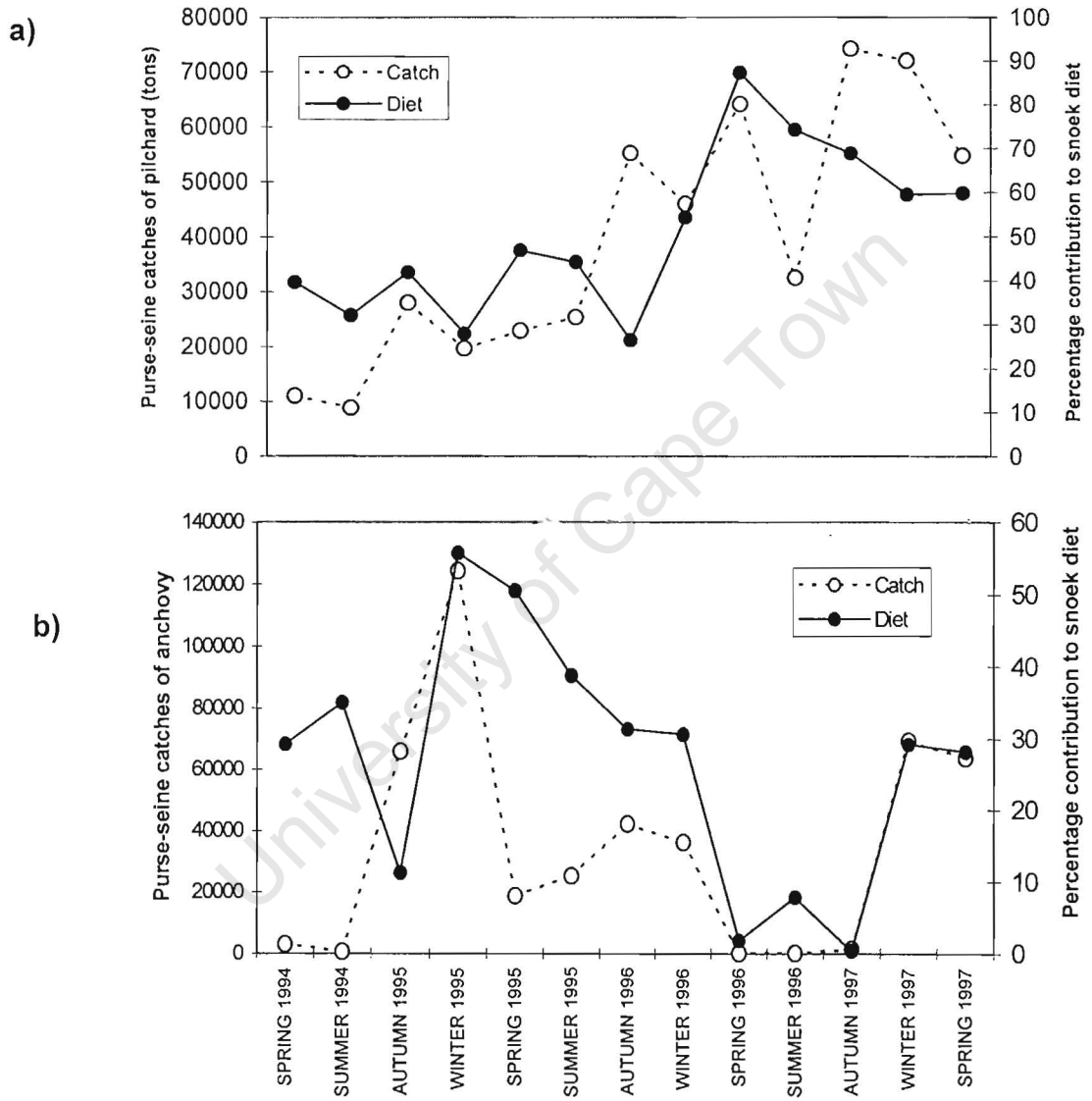


Figure 3.9: Comparisons of purse-seine catches and percentage contributions to snoek diet of a) pilchard, and b) anchovy.

The results of the selectivity test (Figure 3.10), on average, show that snoek seem to have a strong preference for anchovy (mean selectivity, 1994-1997: 1.28 ± 0.6 – mod. Shorigen index), and that the consumption of pilchard is essentially random (mean selectivity, 1994-1997: 0.04 ±

0.19 – mod. Shorigen index). The difference in average selectivity was significant.

(t-test: $p = 0.5 \times 10^{-5}$).

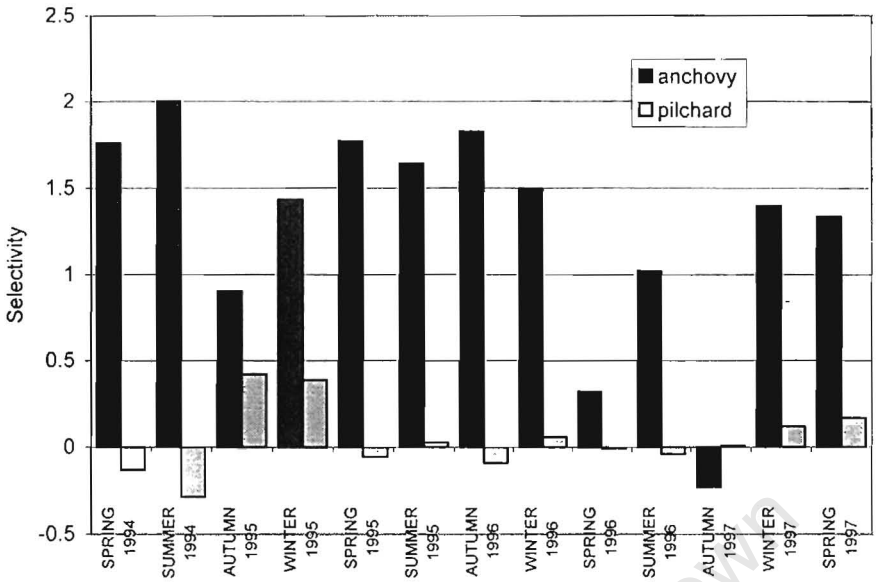


Figure 3.10: Selectivity, as calculated using a modified version of the Shorigen Index (Equation 3.1) for pilchard and anchovy, per month.

DISCUSSION

Seasonal variation

Inshore

The results of the cluster analysis and MDS showed no clear seasonal patterns in the diet of snoek inshore in Region 3. The two principal prey species in this area, (pilchard and anchovy) were essentially available all year round for the four-year duration of the study, with pilchard dominating in percentage weight (Figure 3.3 a)). This trend would appear to confirm present theories (Crawford 1998) that the pelagic regime may be switching from anchovy to pilchard, as indicated by a marked increase in the proportion of pilchard in snoek diet, from the period during which Dudley (1987) conducted his diet study (mid 1980's), when almost no pilchard was present in the diet Anchovy availability was not noticeably greater in the spring and summer months, as predicted, being almost absent in the spring and summer of 1996. In general, the two species seemed to provide a more or less continuously available resource for snoek off the Cape Peninsula. The proportions of these main prey species seemed rather to vary in the diet in correspondence with fluctuations in their relative abundance in the region sampled. This was indicated by their numbers and proportions in the purse-seine catches (Figs. 3.8 and 3.9), and by spawner biomass surveys conducted over the same period (Barange *et al.,* 1999), which will be discussed further below. There were subtle seasonal patterns of availability in the less prevalent prey species in the diet.

Round herring was present in all seasons in snoek diet in this area, with the exception of spring. This time of non-availability to snoek coincides with the peak spawning time of round herring (late winter to early summer), which takes place offshore, meaning that their distribution would not extend into this area at this time (Armstrong and Thomas, 1989; Roel *et al.*, 1994). Availability was generally lower from late 1995 to the end of 1996, which is most likely attributable to reductions in biomass and availability, possibly due to fluctuations in the environment, resulting in unfavourable conditions for round herring in this region.

Mantis shrimps were absent from the diet in winter, which is consistent with their seasonal

Regional (onshore-offshore) variation

Regional differences in diet (between on- and offshore samples) were much greater than seasonal differences. The main difference was the complete absence of anchovy, and the higher proportion of hake, in the offshore diet. Differences are easily accounted for, as the species that did occur in the offshore diet either have much wider distributions than anchovy (e.g. pilchard, round herring), prefer the colder waters offshore (e.g. horse mackerel, which is usually limited to temperatures of 16 – 19 °C), or prefer deeper waters offshore (e.g. hake). In other words, the species that are prevalent in the diet of snoek offshore are those that naturally occur in this area, implying that snoek opportunistically consume what is available.

Inter-annual variation

The results point towards considerable inter-annual variation in the proportions of prey species. Such disparities in abundance and distribution are often largely attributable to environmental fluctuations, which are common in the Southern Benguela, characterised as a rich but variable system (Smale, 1992). Variations are present in both the biotic and abiotic elements in the system, on many spatial and temporal scales (Shannon *et al.*, 1992). Abiotic or climatic factors often have profound effects on the spawning and recruitment success of the species in the system, beginning with primary production and affecting all the species in the food web at some point (Klages *et al.* 1992).

Examples of abiotic fluctuation include factors such as sea surface temperature. This can determine the spawning distributions of species (Aggus, 1979) e.g. adult anchovy will usually only spawn in water cooler than 20 °C, and recruits also prefer cold waters (Crawford, 1989; Roel *et al.*, 1994; Barange *et al.*, 1999). The prevailing currents in a spawning area can determine the successful transport of eggs and larvae to nursery areas. Advective loss of spawning products offshore by unfavourable currents can lead to poor recruitment or even recruitment failure, resulting in a poor year class for the species concerned (Boyd *et al.*, 1998). This has greater impacts on short-lived species such as clupeoids, where poor year classes

several years running, cause a domino effect of continued spawning and recruitment failure due to reduced spawner biomass. Longer-lived species are more 'buffered' to such effects, and poor year classes do not have as great an impact on biomass (Boyd *et al.*, 1998; Cury *et al.*, 2000). Upwelling strength is another important factor in determining spawning and recruitment success. Upwelling, driven by southeast winds on the West Coast, is responsible for the high productivity of the system (Crawford, 1989). Phytoplankton production is promoted and controlled by the upwelling of nutrient-rich waters, providing a food resource for both pelagic fish and zooplankton (Jarre-Teichmann *et al.*, 1998). At times when upwelling strength is inadequate, there are limited food resources for important pelagic species, meaning that their population numbers may decline, or that they may migrate to areas in which conditions are more favourable; leading to locally reduced or patchy availability to predators such as snoek (Pillar, 1986; Crawford, 1989).

The conditions mentioned, as well as many other factors, can all have an effect on the abundance and availability of prey species, resulting in concomitant fluctuations in the diet particularly of adaptable generalist predators, as are seen in this study. The generalist feeding strategy is ideal and thus common in such a variable system. Opportunistic selection, and the ability to adapt to whatever prey is available in the area at the time, means that snoek are able to maintain their success, even if conditions are variable. There did appear to be some degree of preference for anchovy over pilchard (and of clupeoids in general), but certainly not to the exclusion of other species. As seen when comparing offshore and onshore diets, when anchovy was not available, those species that were present were consumed instead.

Links between diet and abundance

Acoustic estimates of spawner biomass for pilchard and anchovy indicated that pilchard biomass marginally exceeded that of anchovy in 1994 and 1995, which is reflected in the results of this study. While pilchard number increased steadily over the study period, anchovy numbers showed major fluctuations, dropping drastically in 1996, but rising again in 1997 (Barange *et al.*, 1999). Broken down seasonally, this pattern was repeated in the diet of snoek, with a sharp

drop in the proportion of anchovy from spring 1996 to autumn 1997 (as reflected in Figure 3.5), when they reappeared in the diet.

Observed inter-annual fluctuations in pilchard and anchovy abundance were mirrored quite closely by snoek diet in the inshore regions. The overall trends in mass caught seemed reflected in the diet, with one or two exceptions, that could be related to predation or selectivity. For instance, a discrepancy between diet and catch occurred for anchovy in 1995, where catches were low, but the proportion in the diet was high. Barange *et al.* (1999) described this as a period of high mortality for anchovy recruits. Judging by their contribution to the diet of snoek, this mortality (and hence reduced availability to the fishery) could have been partly due to wide-scale predation by snoek, which showed a degree of selectivity toward anchovy (particularly in 1995 and early 1996). This period (winter and spring of 1995) also coincided with the spawning season for snoek, which is their time of maximum feeding intensity (Chapter 4). It should also be considered that while catches are a broad indicator of availability, fishing for pelagic species is essentially non-random, and that targeted fishing would produce additional biases in abundance estimates, which would be reflected in these results.

CONCLUSIONS

The diet of snoek shows some subtle seasonal patterns, with regional or depth-determined (inshore / offshore) variation in diet far more pronounced than seasonal variation. Inshore diet fluctuations seemed similar to fluctuations in pilchard and anchovy abundance in the sampling region, as indicated by purse-seine catches. A positive selectivity toward anchovy by snoek was evident.

The two main prey species in the inshore diet (pilchard and anchovy) effectively showed year-round availability to snoek around the Cape Peninsula, contrary to Crawford and de Villiers' (1985) assumptions. This has important implications for the behaviour of the predator, which are discussed in Chapter 4.

It is hoped that the results of this study will have potential practical applications. Trends in the diets of predators, including the catch statistics, are influenced by the abundance of their main prey species (Stouder *et al.*, 1993). The proportions of pilchard and anchovy in the diet of the Cape Gannet (*Morus capensis*) have been significantly correlated with other estimates of abundance (Crawford *et al.*, 1992). The diets of these birds are thus used as measures of the abundance of their main prey species from year to year. The diet of snoek also seems to broadly reflect the natural abundance of its two main prey types, as seen in catch statistics and biomass surveys. This being the case, there is good reason to suggest that it also be monitored and used as a broad indicator of prey abundance. The role of selectivity and an apparent preference for anchovy by snoek imply that while snoek diet could indicate possible regime shifts between pilchard and anchovy (as can be seen in the increase in pilchard in snoek diet from the mid-1980's (Dudley, 1987) to the present), it could not be used as a fine-scale indicator of abundance. This selectivity definitely warrants further investigation, as it may have interesting implications regarding snoek movements, behaviour and adaptations during times where the pelagic regime shifts away from anchovy.

APPENDIX 3.1: Details of all species found as prey items in snoek stomachs, in Region 3, both inshore and offshore. The appearance of prey items in the diet in- or offshore are indicated, as are their habitats.

COMMON NAME	**TAXONOMY**	**IN / OFFSHORE**	**HABITAT**
TELEOSTI			
Pilchard	*Sardinops sagax*	both	pelagic
Anchovy	*Engraulis encrasicolus*	inshore	pelagic
Horse mackerel	*Trachurus trachurus capensis*	both	pelagic
Red eye / round herring	*Etrumeus whiteheadi*	both	pelagic
Hake (shallow-water)	*Merluccius capensis*	adults offshore, juveniles of both spp. inshore	demersal
Hake (deep-water)	*Merluccius paradoxis*		demersal
Lantern fish	*Lampanyctodes hectoris*	offshore	mesopelagic
Buttersnoek	*Lepidopus caudatus*	offshore	pelagic
Chub Mackerel	*Scomber japonicus*	offshore	pelagic
Light fish	*Maurolicus muelleri*	offshore	mesopelagic
Rat tail	*Symorenchus coel*	offshore	demersal
Steentjie	*Spondyliosoma emarginatum*	inshore	demersal
Sole	*Cynoglossus capensis*	both	demersal
John dory	*Zeus capensis*	offshore	demersal
Gnathophis	*Gnathophis capensis*	inshore	pelagic
Clinidae	Species not identified	inshore	demersal
Jacopever	*Sebastes capensis*	offshore	demersal
Saury	*Scomberesox saurus scomberopides*	offshore	pelagic
Sandchord	*Gonorynchus gonorynchus*	inshore	demersal
Pelagic goby	*Sufflogobius bibartus*	inshore	pelagic
Dragonet	*Paracallionymus costasus*	offshore	demersal
Fingerfin	*Chyrodactylus pixi*	inshore	reef
Red harder	*Emmylichthys nitidus*	offshore	demersal
Sole	*Austroglossus capensis*	inshore	benthic
CRUSTACEA			
	Stomatopoda		
Mantis shrimp	*Pterygosquilla armata capensis*	inshore	pelagic
	Euphausiacea		
Krill	*Euphausia lucens*	inshore	pelagic
	Macrura		
-	*Funchalia*	offshore	pelagic
Crayfish	Crayfish plurillae	inshore	pelagic
Pacific prawn	*Pacifia*	inshore	pelagic
	Brachyura		
Crab	Crab larvae	both	pelagic
Mycids	**Mysidacae**	both	pelagic
	Isopoda		
Red isopod	*Paradotia ungulata*	inshore	pelagic
	Amphipoda		
-	*Themisto gaudichaudi*	inshore	pelagic
CEPHALOPODA			
Chokka squid	*Loligo vulgaris reynaudii*	inshore	both (pel and dem)
-	*Todaropsis eblanae*	both	both (pel and dem)
-	*Lycoteuthis?*	offshore	both (pel and dem)
Cuttlefish	*Sepia australis*	both	both (pel and dem)
ANNELIDA			
Bristle worms	Polychaeta	both	benthic

Chapter 4:

Seasonal trends in the feeding intensity and physiology of snoek (*Thyrsites atun*)

Chapter 4

INTRODUCTION

Seasonal physiological and behavioural rhythms

Intrinsic links exist between the physiology, biochemistry and behaviour of fish, and the ecology and environmental conditions of the habitat in which they occur. Thus, in adult fish gonad mass, body condition and fat reserves fluctuate (to a greater or lesser extent), on a seasonal basis as a function of the life-history strategy of the species (e.g. in response to the spawning regime or migration patterns) (Shul'man, 1974). Calendar periods of spawning behaviour have evolved in response to the annual environmental regimes experienced by fish. They have evolved thus in order that the developing young are provided with food and ideal conditions for growth and survival (e.g. avoidance of predation) (Begg and Hopper, 1997). In addition to endogenous physiological rhythms, feeding behaviour and intensity also fluctuate on a seasonal basis in some species, in response to the physiological needs of the fish (Link and Burnett, 2001).

Adaptive responses in physiology and behaviour are intricately associated with seasonal climatic cycles. By remaining relatively plastic and flexible, life-history traits allow the fish to adapt to short-term (intra-annual) fluctuations in the environment, and retain a relative overall stability in population structure. Adaptations to fluctuations in the prevailing conditions, both within a year and from year to year or decade to decade, mean that reproductive success and species survival is ensured.

Spawning

The food consumed and energy stored by adult fish serves three basic functions: baseline metabolism (*e.g.* respiration, movement, foraging, *etc*), somatic growth, and reproduction. Reproduction is described by Schul'man (1974), as the "biological axis" around which seasonal physiological rhythms and processes revolve. The spawning process begins with the differentiation of gonad tissue to form gametes. The gonads then continue to develop through various stages of maturity as spawning approaches, until they reach a stage known as 'ripe -

running' (Table 1, Chapter 5), at which point the gametes are released (Nikolsky, 1963; Shul'man, 1974). In order to determine the state of readiness for spawning in fish, a morphological indicator, known as the gonadosomatic index (GSI) or the coefficient of maturity, is used. This is essentially the mass of the gonad as a percentage of the mass of the fish (minus gonad and gut mass) (Nikolsky, 1963; Sadovy, 1996). In addition to this, visual indices of preparedness are also commonly utilised. These require a subjective judgement of gonad appearance, and usually encompass between five and seven 'stages' (Nikolsky, 1963; Wooton, 1990; Sadovy, 1996).

In fish, reproductive biology and behaviour are highly variable from species to species, but most show some form of distinct stable, repeatable patterns of physiological changes associated with the process (Shul'man, 1974). Some fish may spawn only once a year, some continuously for protracted periods during the year, and others, with intermittent peaks, may spawn year round (Shul'man, 1974; Sadovy, 1996). Some species, known as complete spawners, release all the gametes in a single event (Wooton, 1990). Serial spawners, of which there are two types, release eggs over a period of time. In determinate serial spawners, all the eggs ripen at the start of the spawning season and small proportions are released intermittently. The ovaries of indeterminate serial spawners contain primary oocytes at the beginning of the spawning season, and 'batches' of these ripen to be released at intervals, depending on the female's fitness (Sadovy, 1996). This indeterminate ripening of oocytes could be dependent, in part, on food availability to the spawning female, as they can be reabsorbed by the body in times of need (Shul'man, 1974; Sadovy, 1996).

The stage of preparation for spawning and the physical activity of spawning, are the periods of peak energy expenditure (Shul'man, 1974). The formation of generative tissue, and particularly yolk accumulation in the oocytes of female fish, require that the individuals reach a benchmark fitness level, or condition state, before spawning can take place ((Shul'man, 1974; Wooton, 1990; Slotte, 1999). In indeterminate spawners, this benchmark may have to be reached repeatedly throughout the spawning season, as each batch of eggs is set to ripen (Sadovy,

1996). Increased metabolic activity and the powerful muscular contractions, which occur as gametes are released, mean that the actual act of spawning also demands a lot of energy (Shul'man, 1974). Many species undertake extensive migrations to spawning grounds prior to reproduction, which further adds to the energetic costs of the process (Shul'man, 1974; Slotte, 1999).

Fat reserves

In order to meet the energy requirements for spawning, fat reserves are accumulated in the form of fatty deposits throughout the body. Fat is the most calorie-rich, stable and economical source of stored energy available to any organism (Shul'man, 1974). In fish, it is the major source of energy used in the synthesis of generative tissue, and in females, is often transferred directly to the yolk of developing oocytes to provide an endogenous energy source for the embryo (Wooton, 1990; Sadovy, 1996). Fat can be stored in a number of ways, including deposits in the liver and muscles, attached to the gonads (e.g. in geelbek, *Atractoscion aequidens*), the wall of the intestine and stomach (e.g. in snoek), or in the abdominal cavity (Shul'man, 1974; Griffiths, 1988; Griffiths, 2002).

Due to its close relationship with the changing energy requirements of the fish, fat content is usually highly variable throughout the year (Shul'man, 1974; Lambert and Dutil, 1997a; Slotte, 1999). Because of this, it is a good indicator of the state of well-being of an individual or population at any point during its annual cycle (Shul'man, 1974). Distinct seasonal patterns of fatness are well documented, not only in fish, but in many classes of organism, from invertebrates to mammals (Shul'man, 1974; Slotte, 1999). The period of maximum fatness and highest relative condition in fish usually occurs immediately before gametogenesis and spawning, at the onset of which, both decline drastically (Shul'man, 1974; Wooton, 1990; Godinho, 1997; Slotte, 1999). Fat is measured in a similar way to gonad development, i.e. by means of a visual index, based on a judgement of body fat. A gravimetric index (like GSI) of the mass of somatic fat and liver fat as a percentage of body mass, can also be used (Shul'man, 1974; Lambert and Dutil, 1997b; Slotte, 1999).

Condition

Relative condition factor, also known as the Index of Well-Being, is a morphological indicator closely linked to fat content. This measure shows how healthy or robust an individual is, using body mass as a gauge of fitness. It is used in terms of a comparison to an established specific length-weight relationship for the fish. Actual weight values are compared with expected values as calculated by the length-weight formula (Hynes, 1950; Shul'man, 1974; Blackwell *et al.*, 2000). Temporal changes in condition can then be detected in the fish population in an area (Lambert and Dutil, 1997 a, b). Clearly observable seasonal patterns of fluctuation in the condition of populations are recognised in many fish species (Lambert and Dutil, 1997b; Godinho, 1997; Slotte, 1999). As the fat content contributes to body weight, it most likely exerts some influence on condition factor, and the two attributes often follow near-identical seasonal trends (Hynes, 1950; Shul'man, 1974; Lambert and Dutil, 1997b).

Feeding intensity and foraging behaviour

In order for spawning to begin, adequate fat reserves must exist and an individual must attain a minimum condition factor (Shul'man, 1974; Link and Burnett, 2001). If this condition level is not reached in time for spawning or overwintering, it can mean a drastic reduction in fecundity or even result in mortality (Lambert and Dutil, 1997 a, b; Link and Burnett, 2001). The timing of spawning events depends on the attainment of these minima (as well as environmental cues or triggers), and the ability to accumulate these reserves depends, in turn, on the quality and quantity of the resources available to the fish during their periods of intensive feeding (Hynes, 1950; Shul'man, 1974; Godinho, 1997). Many serial spawners (such as snoek) are known to continue feeding intensively throughout spawning, due to the continuous energy demands as egg batches ripen for release (Shul'man, 1974). Despite continued foraging in these fish, fat reserves and condition continue to decline, and reach a minimum level as spawning slows and ceases (Shul'man, 1974; Lambert and Dutil, 1997b).

Changes in food consumption and feeding intensity are factors that often show some form of annual cyclical rhythm in fish (Lambert and Dutil, 1997 a, b; Slotte, 1999; Link and Burnett, 2001). These are not always attributable to behaviour and can be due to factors such as fluctuating food availability, or even overestimation of food consumption by researchers, as evacuation rate can fluctuate with temperature and other environmental conditions (Shul'man, 1974). Studies do indicate, however, that even where both these potential sources of error remain constant, food consumption still varies (Shul'man, 1974; Wooton, 1990).

In iteroparous species, two major feeding strategies, the 'ramper' and 'rester' strategies were described by Link and Burnett (2001), and links were drawn between feeding and spawning. These strategies represent two ends of a continuum, in the middle of which are found 'indeterminate' species, where no noticeable relationship between gonad development and feeding intensity occurs. Set periods of intensive feeding have been indisputably linked with the build-up of fat reserves and increase in condition in the fish (Wooton, 1990; Sadovy, 1996). It is thought that these patterns of feeding intensity have evolved to match the seasonal availability of food resources, and the post-spawning conditions in which eggs and larvae must survive (Link and Burnett, 2001). This means that the relationship between feeding and maturity stage is intrinsic to the life cycle and survival of fish.

1.The 'rester' pattern refers to fish which cease feeding during their spawning period (e.g. Atlantic cod, *Gadus morhua*; chub mackerel, *Scomber japonicus* and silver hake, *Merluccius bilinearis*). These fish resume feeding after spawning during the spent and resting stages of gonadal development (stages 2 and 5, Table 5.1, Chapter 5), allowing them to restore energy reserves. It has been proposed that autumn-winter spawning species would show this feeding pattern, as if spawning occurs in the colder months, growth and metabolic costs would be lower and would be recovered in warmer months, during times of high productivity (Link and Burnett, 2001)

2. The 'ramper' pattern is evident in fish which undergo a period of intense foraging that can last from weeks to months, prior to and during spawning, during the 'ripe' and 'ripe-running' stages of gonadal development (stages 3 and 4, Table 5.1, Chapter 5). The period of maximum fatness and highest condition thus occur immediately before spawning (Shul'man, 1974; Wooton, 1990; Godinho, 1997; Slotte, 1999). In some species, this prespawning period is characterised by feeding aggregations, or followed by migration of adults to spawning areas. After spawning, the fish return to 'normal' feeding intensities. It was proposed that fish exhibiting a 'ramper' pattern would be spring-summer spawners, during or after times of high productivity (Link and Burnett, 2001)

The seasonal physiological rhythms discussed above, have evolved in tune to the prevalent environmental and ecological conditions, to optimise the fitness and reproductive potential of the species concerned (Shul'man, 1974; Wooton, 1990). Once quantified, these attributes allow a degree of predictability regarding a fish species. For example, feeding aggregations or spawning migrations may allow the design and implementation of management measures such as regional or seasonal restrictions (Link and Burnett, 2001).

AIMS

The aims of this chapter were to investigate the seasonal physiological rhythms and seasonal feeding intensity or prey consumption in snoek (*Thyrsites atun*), off the west and south-west coasts of Southern Africa - a part of the Southern Benguela ecosystem. This is an eastern-boundary current system, characterised by seasonal upwelling events, and high variability, both biotic and abiotic (Shannon *et al.* 1992). Seasonal patterns in feeding intensity and meal size were investigated in a small section of the distribution range of snoek (Chapter 1), which occurs in Region 3 (Figure 4.1), covering the inshore waters around the Cape Peninsula. Physiological aspects such as gonad maturation, fat content and relative condition were examined over a slightly wider geographical range (Regions 3 and 4, inshore and offshore, Fig. 4.1).

Estimates of feeding intensity are useful, as they can be used in the construction of trophic models in an ecosystem. Seasonal differences in feeding intensity need to be identified and quantified in order to standardise annual consumption estimates (Whipple *et al.*, 2000). If differences do exist, estimates from any particular season must be weighted, in order that mean annual consumption is correctly calculated (Palomares and Pauly, 1989). Consistent patterns of aggregation related to spawning and feeding, can also be useful in predicting fish movements (Link and Burnett, 2001). Seasonal trends in feeding intensity and consumption were investigated in relation to spawning physiology in snoek. Snoek are indeterminate serial spawners, with a spawning period extending from early winter to late spring/early summer (Chapter 1). Spawning occurs offshore, although Griffiths (2002), postulates that female fish may move inshore on the West Coast, to feed between spawning bouts (Appendix 4.4). This being the case, the prediction is that snoek would exhibit the 'ramper 'pattern, and continue to feed during spawning, as is typical of serial spawners (Shul'man, 1974). The proportion of fish feeding, as well as the relative amount of food consumed, was investigated seasonally.

Annual cyclical rhythms of condition and fat content were investigated in relation to gonad maturation for the period concerned, although they have been previously documented (Griffiths, 2002). Changes in relative condition factor were investigated from year to year to see if there were any correlations with prey availability (Chapter 3). Relative condition was first researched by Nepgen (1979a), who found that peak condition in this species occurred before spawning in autumn, after which it declined markedly. Fish were found to have low body oil and protein content during and after spawning, and that these levels gradually rose during summer and autumn as relative condition recovered (Rapson *et al.*, 1944, cited by Nepgen, 1979b). Griffiths (2002), comprehensively documented the life history of snoek, including patterns of fat content, GSI and condition. In his study, these factors were mostly calculated for combined seasons, i.e. spawning / non-spawning, or per month. In this study, the aim is to relate physiological trends and feeding intensity, on a seasonal basis. It is hoped that this will produce a more comprehensive picture of the linked inter-annual rhythms in this species, and hence enhance our knowledge of its ecological role on a more fine scale.

METHODS

Sample collection

Snoek were sampled along the South African coastline, which was divided into seven sampling sub regions (0-6, Figure 4.1), from Port Nolloth to Mossel Bay. Sampling was conducted by Marine and Coastal Management from September 1994 - May 2001, producing an extensive database on snoek. The data used for seasonal analyses in this chapter are a subset of this database, collected from September 1994 - January 1998, where sampling was continuous for all consecutive seasons.

The fish were collected in two ways: 'Inshore' samples (★, insert, Figure 4.1) were collected by hand-line fishing, either by research staff or by the commercial line-fishery. Line-caught samples were generally fished at depths less than 60 m, by small fishing vessels operating close to the shore, and will be referred to as 'inshore' samples hereafter.

'Offshore' samples (✕ on Figure 4.1) were gathered by trawling by the commercial demersal trawl fishery or on pelagic and demersal biomass research surveys. For the most part, trawled samples were caught at depths greater than 150 m, and thus occurred further offshore, generally between the 100 m - 450 m isobaths. For the purposes of this study, all samples referred to as 'offshore' were collected in this manner. The specific trawl methods are described in detail by Griffiths (2002)

Biological sampling of the fish involved measuring the fork length to the nearest millimetre, and the total mass to the nearest gram. The fish were then dissected and sexed. Gonads were removed and weighed to the nearest 0.1 g. The stomachs were removed, and total stomach content wet weight was recorded and used to calculate feeding intensity.

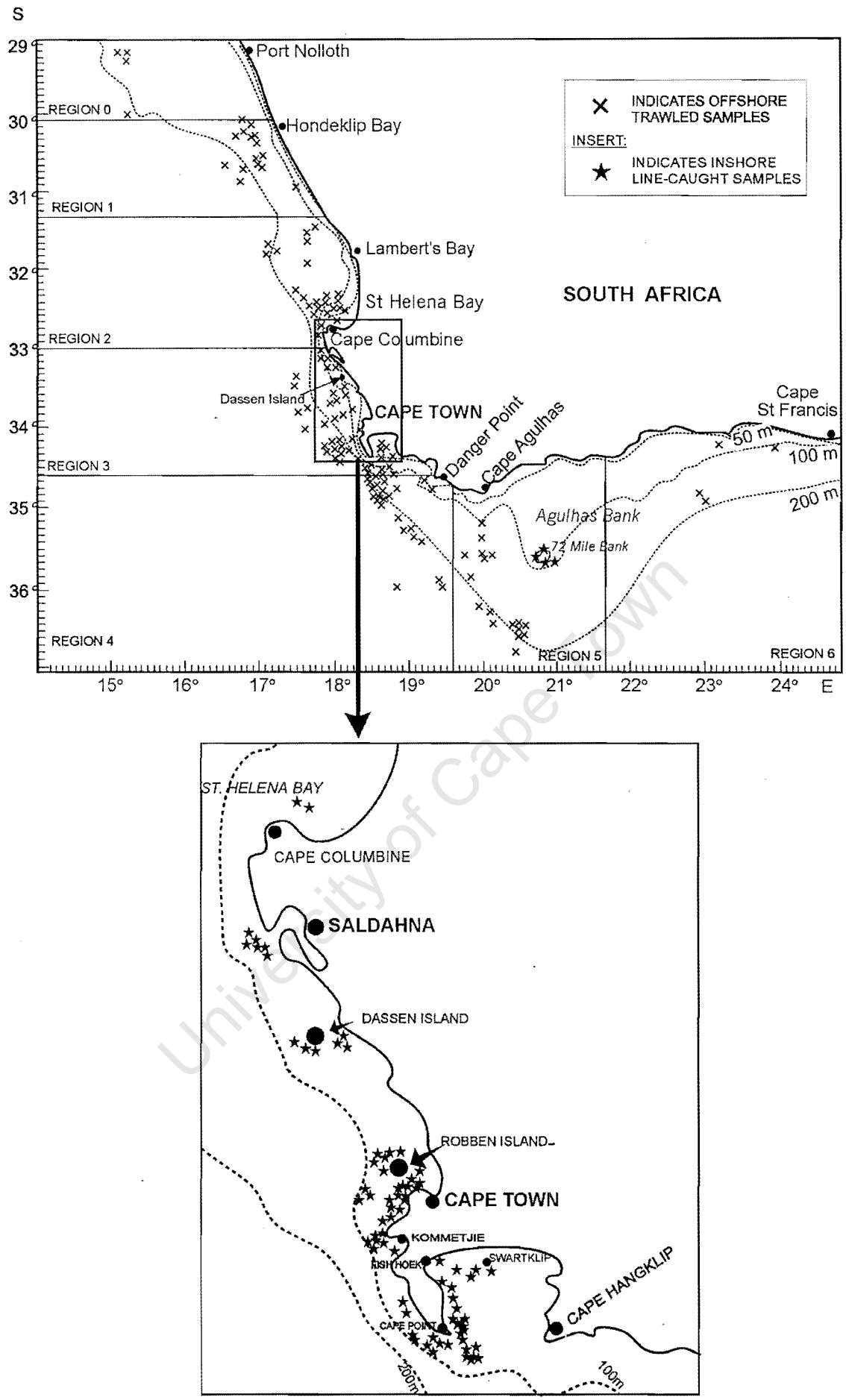


Figure 4.1: Map showing sampling locations of offshore samples (main map), and inshore samples insert). Only samples in Region 3 were used in feeding intensity calculations. Samples from Regions 3 and 4 were used in GSI and fat content calculations. Relative condition factor was calculated using all samples.

A visual index of the superficial fat on the stomach was recorded. Fat is amassed in the form of three longitudinal mesenteric bands along the outer wall of the stomach (Griffiths, 2002) . Indices were assigned according to the following criteria, of which photographs appear in Appendix 4.1:

Table 4.1: Index used to describe the fat classes of snoek based on visual assessments of superficial stomach fat . (See Appendix 4.1 for photographs of each fat class)

FAT CLASS	PHYSICAL DESCRIPTION
0	No fat
1	Bands barely visible, up to 2 mm wide
2	Narrow white bands clearly visible, around 5 mm wide.
3	Bands take on wavy appearance, are wider (7 – 10 mm) and deeper.
4	Fat in wide (15 – 20 mm), wavy, corrugated bands running longitudinally. Width such that subsequent bands touch when the stomach is not fully distended

Analysis

All the parameters measured for snoek were analysed on a seasonal basis. The year was divided into seasons as follows: Autumn: March - May; Winter: June – August; Spring: September – November; Summer: December - February (of the following year).

In this analysis, only adult fish (fork length greater than 700 mm - Chapter 3) were used to avoid the introduction of variation caused by the low gonad masses of immature specimens. Many of the seasonal patterns seen in fish are related to spawning (Shul'man, 1974), and thus the use of sexually inactive fish would be inappropriate for this study. The exception to the benchmark length measurement of 700 mm was for the calculation of the length-weight relationship, used to measure relative condition, where a minimum fork length of 500 mm was used. For all measurements, male and female fish were analysed separately, owing to possible differences in reproductive costs and strategies between sexes. The sample sizes used are indicated on the figures with which they are associated in the results section.

Feeding

The seasonal rate of prey consumption for snoek was estimated by calculating the percentage of fish with food in their stomachs, as well as the mean meal size of the fish with stomachs containing food. This was done using the same data subset used in the calculation of diet, i.e. inshore in Region 3.

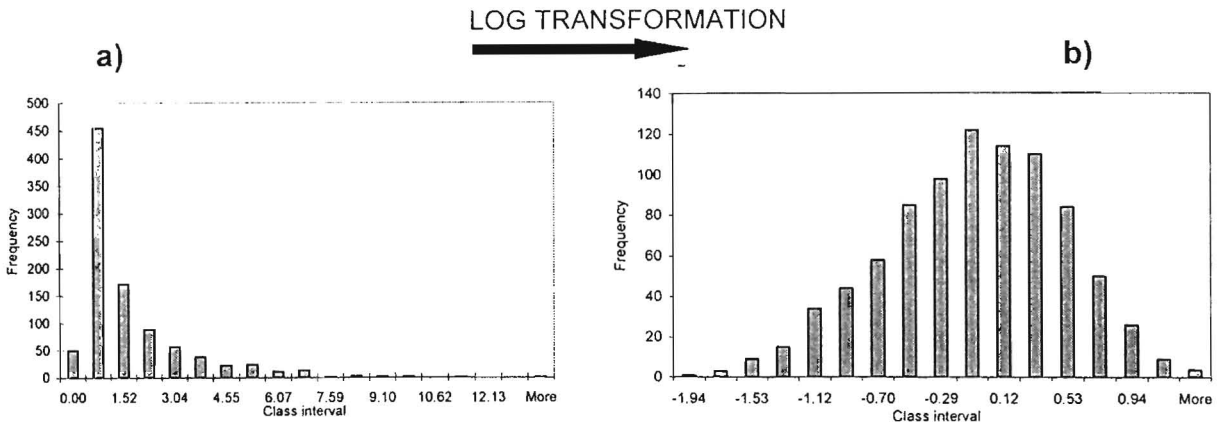
The percentage of fish with stomachs containing food simply involved determining the proportions of empty stomachs for the whole data set. Data were pooled over years, as a χ^2 tests found no significant difference in seasonal proportions between years (Female: spring – p = 0.60; summer- p = 0.06; autumn- p = 0.69; winter – p = 0.90. Male: spring – p = 0.06; summer- p = 0.07; autumn- p = 0.45; winter – p = 0.78)

The meal size per fish, or 'stomach fullness', as it will henceforth be known, was calculated by means of a consumption index, given by the equation:

$$\textbf{Stomach Fullness} = \frac{\mathbf{SM}}{\mathbf{FM - GM}} \times 100 \qquad \text{.....equation 4.1}$$

Where **SM** is the total mass of the stomach contents, **FM**, the total fish mass, and **GM**, the gonad mass. The gonad mass was subtracted to reduce the variation caused by changing gonad size and weight throughout the year. Stomach fullness was calculated only for fish with stomachs containing food, and males and females were separated and tested for differences in feeding intensity.

Stomach fullness data was tested for normality, and was found to be non-normal. A log transformation was thus undertaken to normalise the data (Figures 4.2 a) and b)), allowing the use of parametric statistical testing.



Figures 4.2 a) and b): show frequency distributions of a) the untransformed stomach fullness data, and b) the data after log transformation, resulting in a normal distribution, on which parametric tests could be performed.

An analysis of variance (ANOVA) found between-group (seasons) variation significantly higher than within-group (years) variation (Female: $F = 7.85$; $p = 0.37 \times 10^{-4}$; Male: $F = 4.52$; $p = 0.004$), and data were thus pooled over years and the means plotted as a histogram. Analyses of variance were performed on the pooled data to test where the most highly significant differences between seasons lay.

Gonadosomatic index (GSI)

The seasonal patterns in gonad maturity of snoek were calculated and presented by Griffiths (2002), for the period 1994 – 1997. Using a regional subset of the same data, GSI was recalculated for this period. The equation is as follows:

$$GSI = \frac{GM}{FM - (GM + SM)} \times 100 \qquad \text{.....equation 4.2}$$

Where **GM** is gonad mass, **FM** total fish mass, and **SM** stomach mass.

The data used for the calculation of GSI were taken from Regions 3 and 4, inshore and offshore (Figure 4.1). The data could be pooled as gonad mass changes more slowly than a characteristic such as diet and would probably not vary as much over this limited region as diet would. Thus, allowances could be made for the movement of fish over a larger area. These data

were pooled over years, as between-group (seasons) variation was again found to be significantly higher than within-group (years) variation (Female: $F = 218$; $p = 0.8 \times 10^{-107}$; Male: $F = 151$; $p = 0.15 \times 10^{-65}$). No statistical testing was deemed necessary to further indicate the spawning pattern and differences in GSI between seasons, which is already described in detail by Griffiths (2002).

Condition

Relative condition is a measure of how the mean body weight of the individuals in a population change over time, relative to the weight as calculated by an established condition or length-weight relationship. It involves establishing a baseline length-weight relationship and then gauging the difference between the calculated and actual observed mass values (Lambert and Dutil, 1997, a and b,; Godinho, 1997; Blackwell *et al.*, 2000). The data used here were taken from all regions, for all fish with a fork length greater than 500 mm, for which stomach mass and gonad mass had been recorded. The baseline length-weight relationship was established with the aid of SOLVER® for Windows™, and is described by the equation:

$$\mathbf{W = aFL^b} \qquad \text{.....equation 4.3}$$

Where **a** and **b** are species-specific constants, **FL** is fork length, and **W** is fish body mass, described by the equation:

$$\mathbf{W = FM - (SM + GM)} \qquad \text{.....equation 4.4}$$

Where **FM** is total fish mass, **GM** gonad mass and **SM** refers to stomach content mass. SOLVER® was used to calculate values for the constants **a** and **b**, which minimise the sum of squares (SS) difference between the observed mass (actual values) and the expected mass (calculated using the equation, with hypothetical **a** and **b** values). This is done through numerous iterations of the data, using hypothetical constant values until the values giving the minimum SS are reached. The calculated length-weight values represent the baseline condition mentioned earlier. Relative condition factor (**K**) is then calculated according to the equation:

$$K = \frac{W_{obs}}{W_{exp}} \qquad \text{.....equation 4.5}$$

Where, W_{obs} is observed fish mass and W_{exp} expected fish mass. The values for K were then averaged per season for each year. The data were tested for normality, and found to conform (Figure 4.3), allowing the use of parametric statistical testing.

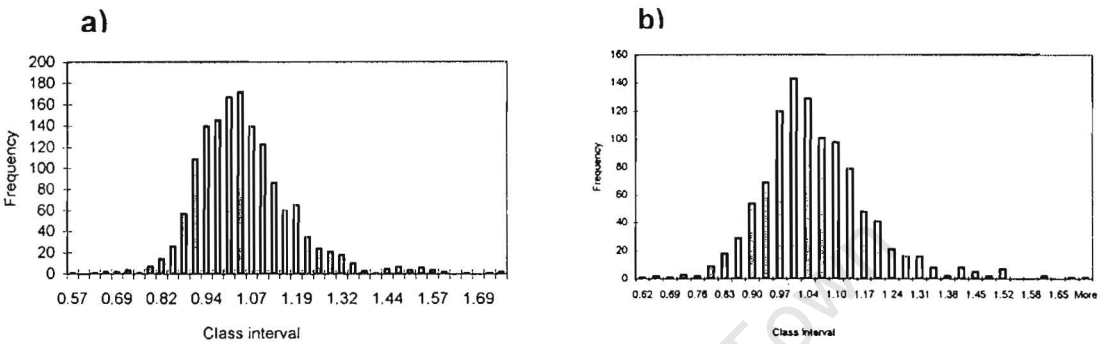


Figure 4.3: Histograms showing the frequency distributions of condition data for a) female and b) male snoek. These distributions approximate normal distributions, and parametric tests were considered appropriate.

ANOVA's found that no significant difference existed for the male and female data sets (F=0.7; p=0.4) and that between-group (seasons) variance was significantly higher than within-group (years) variance for data grouped seasonally, (Male and female data: F= 151; p = 0.69 x 10^{-66}), so data were pooled over years. ANOVA's were then performed to test where the most highly significant differences between seasons lay.

Fat content

The proportions of fish with each fat stage (0 – 4, as described in Table 4.1 and Appendix 4.1) were calculated and plotted as a stacked bar graph for male and female fish for each season. Fat content (per stage) usually has a turnover period of around 5 - 9 days, meaning that extensive spatial ranging could occur (Shul'man, 1974). Thus, data were taken from Regions 3 and 4, inshore and offshore, the wider range applicable, as for GSI and condition. Data were pooled over years and χ^2 tests were used to test for differences in these proportions between seasons and between male and female fish.

RESULTS

Feeding

Figure 4.4 shows the proportion of fish with food in their stomachs. The similarity of these percentages from year to year, between seasons, was very close (results of χ^2 tests appear in the 'Methods' section). The diagram indicates that in winter and spring (during spawning), most of the fish were feeding (± 80% and 65% respectively), followed by the period immediately preceding spawning (±60%), namely autumn. The lowest percentage occurred in summer (±35%). The percentages of females with stomachs containing food were marginally higher than males in autumn and winter, but not significantly so (χ^2, $p = 0.6$). Bearing in mind that sampling was not restricted to any specific time of day (i.e. when the fish were feeding), and was essentially random throughout the years, these results clearly show a change in food consumption or feeding intensity from season to season.

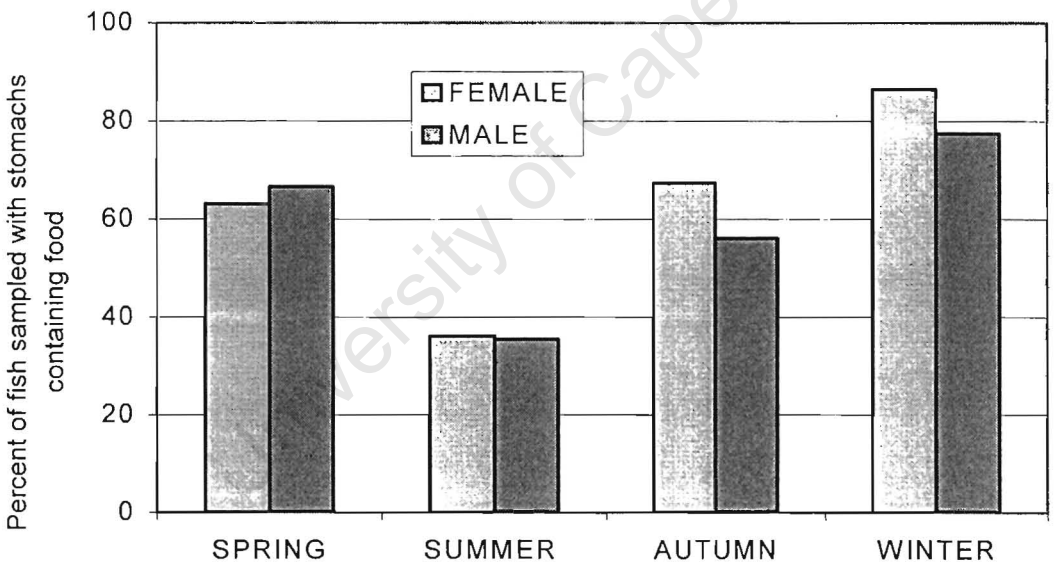


Figure 4.4: The percentages of snoek (> 700mm FL) with stomachs containing food over seasons from 1994 - 1997.

The mean stomach fullness (Figure 4.5) for male and female fish, as calculated by equation 4.1 shows a remarkably similar pattern to that of food consumption. The highest degrees of 'fullness' occurred in winter and spring, with lower levels in summer and autumn.

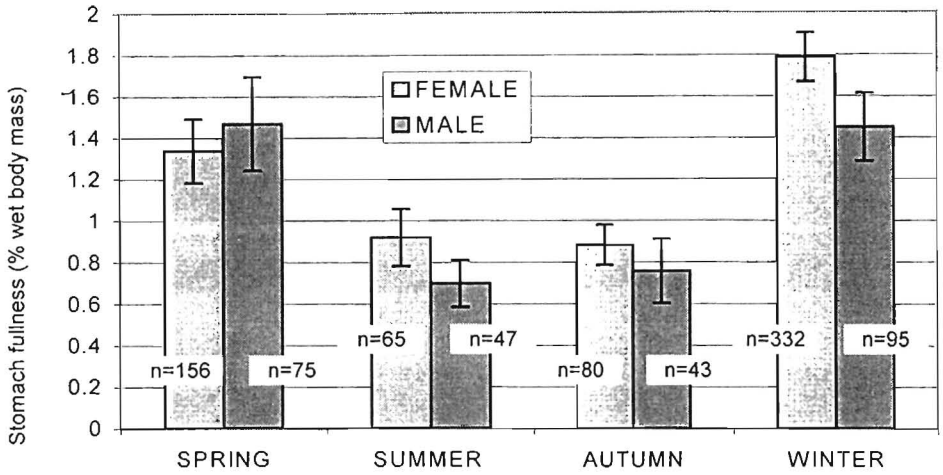


Figure 4.5: Seasonal stomach fullness as a percentage of fish mass (minus gonad mass), per season over all years combined for Region 3. The vertical bars indicate the variance of each sample.

An ANOVA found between-group variation to be greater than within-group variation for both sexes (FE: F=7.85; p=0.0003 and MA: F=4.5; p=0.004). There was no significant statistical difference between males and females, except in winter, where female fullness was significantly higher than male fullness (F=3.9; p=0.05).

Table 4.2: ANOVA values for stomach fullness (the number of asterisks indicate the level of significance, e.g. * = 10^{-2}, ** = 10^{-3} and so on)

FEMALE	SPRING	SUMMER	AUTUMN	WINTER
SPRING		F= 0.01; p=0.8	F= 4.1; p=0.04	F= 7.97; p=0.002
SUMMER	0		F= 0.0047; p=0.95	F= 12.5; p=0.0004
AUTUMN	*	0		F= 14.3; p=0.0002
WINTER	**	***	***	
MALE	SPRING	SUMMER	AUTUMN	WINTER
SPRING		F= 3.16; p=0.07	F= 4.8; p=0.03	F= 0.75; p=0.3
SUMMER	0		F= 0.28; p=0.59	F= 7.7; p=0.006
AUTUMN	*	0		F= 10.16; p=0.001
WINTER	0	***	***	

Table 4.2 shows the results of ANOVA's, where it is evident that the most highly significant statistical differences between seasons occurred between summer and winter, and autumn and winter, for both male and female fish. There was also a significant difference between autumn and spring for both sexes, as there was between winter and spring for females. Snoek therefore fed more frequently and ate larger meals in winter and spring, than in summer and autumn. The

significantly higher feeding intensity and proportion of fish feeding during the spawning months is indicative of a 'ramper' feeding strategy (Link and Burnett, 2001).

Gonadosomatic Index

Figure 4.6 shows the mean gonadosomatic index values for male and female fish by season. In accordance with the spawning period described by Griffiths (2002), the values were lowest in summer, and began to climb in autumn as the gonads matured in preparation for spawning. Values peaked in winter and spring, during the spawning period. Griffiths (2002) describes the entire spawning period as occurring from May to November, with peak spawning from June to October.

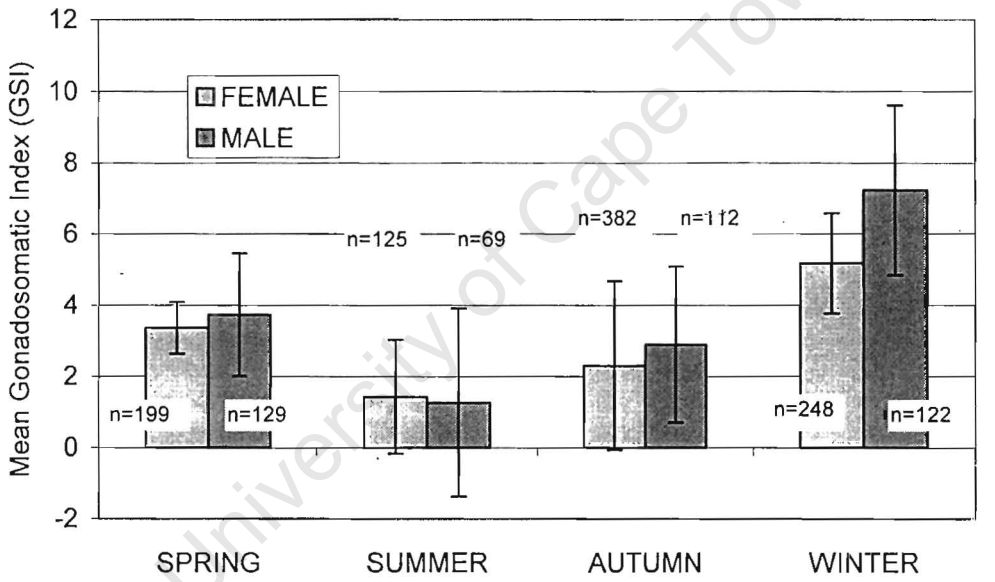


Figure 4.6: Mean GSI values per season for all years combined, Regions 3 and 4. Error bars indicate standard deviation

Condition

Relative condition of adult snoek showed a distinct seasonal rhythm, peaking in autumn and showing low values in spring (Figure 4.7) in all regions over the four-year period. The values for the constants **a** and **b** in equation 4.3 were: **a** = 2.8 and **b** = 0.18 x 10^{-4}, as per Equation 4.3.

The trend in relative condition factor is inverse to those seen for feeding intensity, stomach fullness and GSI. Condition began to increase in summer, and peaked in autumn, prior to

spawning. During peak spawning in winter, condition dropped sharply, reached its lowest point in spring. This trend is consistent with the reproductive costs incurred by the fish in gonad development. An ANOVA found no significant difference in values for male and female fish (F=0.7; p=0.4).

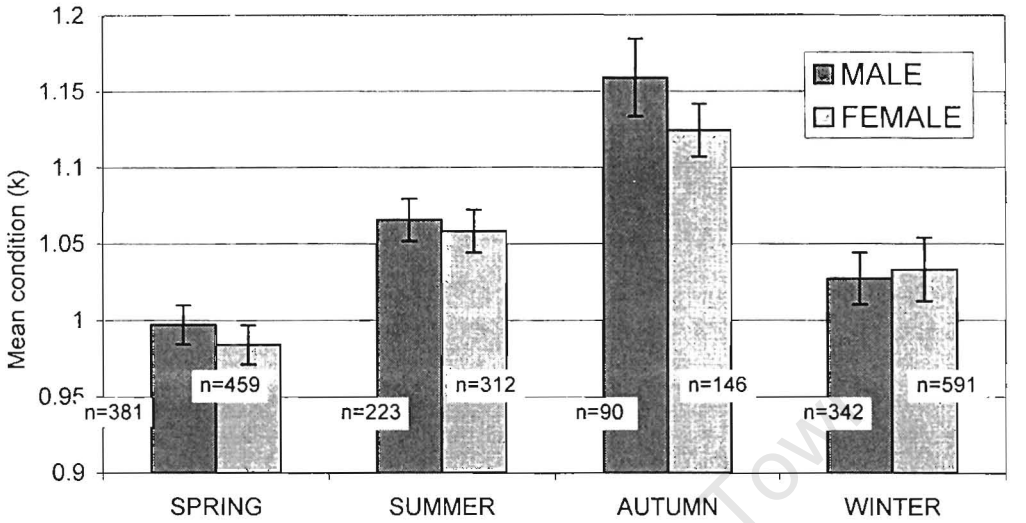


Figure 4.7: Histogram showing the change in the mean condition factor of snoek over seasons for all years combined. Error bars indicate variance values.

The results of the ANOVA's indicating significant differences in condition factor between seasons, are shown in Table 4.3. The most highly significant difference for both sexes was between autumn and spring, followed by spring-winter and spring-summer.

Table 4.3: Results of ANOVA's performed to test that difference in condition between seasons (F crit = 3.85).

FEMALE	SPRING	SUMMER	AUTUMN	WINTER
SPRING		F = 77.2 p=0.97 x 10^{-17}	F = 156.0 p=0.46 x 10^{-31}	F = 26.52 p=0.32 x 10^{-6}
SUMMER	*****		F = 28.57p=0.14 x 10^{-6}	F = 6.9 p=0.008
AUTUMN	*******	***		F = 48.0 p=0.89 x 10^{-11}
WINTER	***	**	****	
MALE	SPRING	SUMMER	AUTUMN	WINTER
SPRING		F = 50.05 p=0.42 x 10^{-11}	F = 125.7 p=0.51 x 10^{-25}	F = 11.03 p=0.0009
SUMMER	****		F = 32.57 p=0.27 x 10^{-7}	F = 12.38 p=0.0005
AUTUMN	*******	***		F = 65.1 p=0.72 x 10^{-14}
WINTER	**	**	*****	

The seasonal trend in condition from year to year remains constant (Figure 4.8), but overall condition appeared to be higher in 1995, particularly in male fish. This could indicate a

physiological response by the population to environmental conditions or food availability.

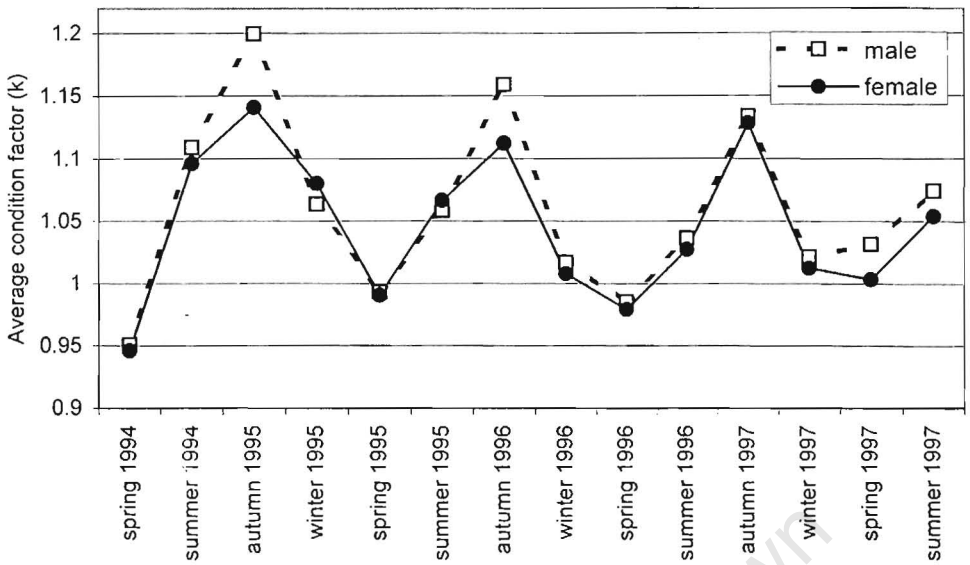


Figure 4.8: Mean condition factor plotted per season over four years, showing the variation in condition from year to year.

Fat content

As anticipated from the trends in condition, snoek had the highest levels of intestinal fat deposits in autumn, followed by summer and the lowest levels in winter and spring (Figure 4.9).

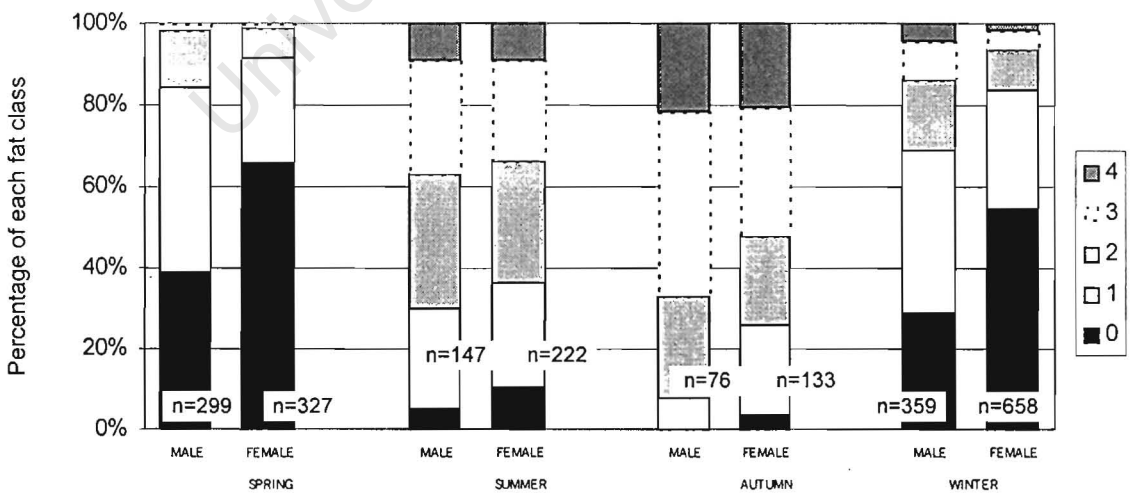


Figure 4.9: Proportions of fish with each fat level for each season over all years.

Chi squared tests revealed that highly significant differences in the five fat proportions existed

between seasons (males: $p=0.32 \times 10^{-83}$; females: $p=0.24 \times 10^{-97}$). Spring and winter were dominated by fish that had fat classes of 0 (spring: males – 39%, females – 66% winter: males – 29%, females: 55%) or 1 (spring: males – 45%, females – 26% winter: males – 40%, females: 29%). In summer there was an even spread of the proportions of fish with classes of 1(males – 24%, females – 26%), 2 (males – 33%, females – 30%) and 3 (males – 28%, females – 25%). In autumn, the highest fat levels were seen, with class 3 dominant (males – 45%, females – 32%), followed by classes 4 (males – 21%, females – 20%) and 2 (males – 25%, females – 23%).

This trend reflects that of relative condition, to which it is closely linked (Shul'man, 1974). A build-up of fat reserves occurred in autumn, in preparation for spawning, with a complete depletion after spawning in spring. Also notable was the significant difference in proportions between male and female fish in winter and spring. Chi squared tests showed that females and males had significantly different percentages of each fat class in winter ($p= 0.81 \times 10^{-13}$), spring ($p = 0.33 \times 10^{-8}$), with no significant difference in summer (p=0.5) and autumn (p=0.06). There were significantly more female fish than males with zero fat content in winter and spring, which may indicate a higher reproductive cost in females.

DISCUSSION

Seasonal rhythms

The results of the Chi squared tests for fat content and ANOVA's of stomach fullness and condition in snoek, demonstrate that these characteristics show distinct seasonal patterns of fluctuation in the Southern Benguela. These cycles are almost certainly related to the spawning regime of the species, which is summarised in terms of GSI values (Figure 4.6) (Link and Burnett, 2001). In accordance with the 'ramper' feeding strategy, the feeding intensity in snoek appears to reach a maximum during the spawning period (Link and Burnett, 2001). In winter and spring, both the proportion of fish feeding and the mean meal size are at a maximum, and values for this period differ significantly from those during the rest of the year. Continued or intensive feeding such as this is common in serial spawners, and particularly in indeterminate serial spawners such as snoek, as the cost of continued oocyte maturation is extended throughout the spawning season (Shul'man, 1974, Sadovy, 1996). The proportion of fish feeding in autumn, prior to spawning, is on a par with the percentage feeding in spring, however the stomach fullness was lower in comparison.

The energetic costs of reproduction in snoek are reflected in the trends in condition factor (Figure 4.7) and fat content (Figure 4.9). These attributes both showed peaks in autumn prior to spawning, although feeding intensity did not peak concurrently. In winter, both declined drastically when feeding was at maximum intensity, meaning most of the energy consumed was being directly channelled into the reproductive process. It should be noted here that perceived feeding intensity and meal size can be affected by changes in environmental conditions. For instance, colder water temperatures in winter can slow digestion and evacuation rates leading to an overestimation of stomach fullness and percent stomachs containing food (Shul'man, 1974; Wooton, 1990). It is thought that in this instance, the increased metabolic and muscular activity, and higher energy demands associated with spawning probably precluded this from being the case. If anything, metabolic rate, and therefore evacuation rate, would most likely be increased at such a time in the fish's annual cycle. In addition, the significantly higher feeding intensity in females relative to males would almost certainly not have been evident if stomach

fullness and the proportion of fish with food in their stomachs were affected by water temperature. A trawl survey of the distribution of snoek over a range of temperatures, in both summer and winter, showed that the majority of fish were caught at a temperature of 8 °C, indicative of a preferred thermal range in the species (Appendix 4.2). This consistency in snoek distribution with temperature would further indicate that digestion rate was probably not significantly affected by water temperature.

Snoek (particularly the males during spawning) showed a slight decline in condition over the four years of this study (Figure 4.8). Because it is more noticeable in males during spawning times, this may have been due to a reduced prey biomass or quality of food available to them on the offshore spawning grounds, as females move inshore to feed (Griffiths, 2002).

Based on two clear facts, the results of this study would seem to indicate that the costs of spawning are much higher for female snoek than for males, resulting in a need for feeding migrations.

1. The fat content of females is significantly lower than that of males during spawning (Figure 4.9), despite the fact that,
2. females consume significantly more food during this period (winter, Figure 4.5).

In terms of the differences in costs of spawning to each of the sexes, females would possibly require high quality food in order to amend continued condition decline caused by the huge energy expenditure necessary for continued intermittent egg production. In many fish species, fat utilisation is much higher in female fish during gonad maturation, as the costs of oogenesis and oocyte development far outweigh those of spermatogenesis (Shul'man, 1974; Wooton, 1990; Sadovy, 1996; Slotte, 1999). This is probably the case in intermittent serial spawners, where vitellogenesis is repeated throughout the spawning season (Sadovy, 1996). In fact, fat or oil is often directly transferred to the yolk of the developing egg. It has been demonstrated that the period of gonad maturation, particularly in serial spawners, is often concurrent with intensive feeding by females (Shul'man, 1974; Wooton, 1990), which would certainly seem to be the case

for snoek. Inshore migrations by females, discussed below, and the positive selection of anchovy (Chapter 3) would seem to indicate an active search by the predator for high-energy food, which would ensure spawning success.

It is acknowledged that the spawning frequency of male snoek is not known, and thus the sexes cannot be quantitatively compared, but the frequency of gamete release is almost certainly higher than that of females. This would mean more frequent gametogenesis at a lower cost, in males. Judging from the decline in fat reserves and condition, the overall costs of spawning do appear to be higher in females.

Sex ratio, diet and the costs of reproduction

The near-constant availability of energy-rich pelagic clupeoids to snoek around the Cape Peninsula (Chapter 3) potentially plays a very important role in their life cycle and spawning behaviour. Griffiths (2002) theorises that this resource is utilised by female snoek during the spawning season. Sex ratios inshore in Regions 0 – 3 (Appendix 4.3), seem to confirm the theory that female snoek migrate inshore on the West Coast between successive spawning bouts, in order to feed. Appendix 4.4 shows that females are dominant inshore on the West Coast (almost three females to one male), and males offshore on the spawning grounds (two males to one female) during winter and spring. During times of highest feeding intensity – winter, spring and autumn - females also dominate inshore in Region 3 (Figure 4.3). Several interesting implications arise when this trend is considered:

1. As established, spawning success in fish is intimately linked with food supply in the pre-spawning period when fat reserves are built up, and in snoek, during the spawning period as well. Successful storage and maintenance of energy reserves is dependant not only on the quantity of food available, but also on the quality of that food (i.e. protein and fat content, amino acids and trace elements) (Nikolsky, 1963; Shul'man, 1974). For snoek, the presence of high quality food (pilchard and/or anchovy) is not only necessary for the build-up of reserves, but also for the success of the spawning process (hence female migration) in this

population. It is possible that snoek in this resource-rich upwelling region have a higher overall fecundity compared with those snoek whose main food source has a lower energy content (e.g. Australian snoek, which feed mainly on euphausiids (Blackburn, 1956)). The timing and length of the spawning period and factors such as batch size and spawning frequency could be partially dependent on the year-round availability of these clupeoids to snoek on the western and south-western coasts of South Africa. In addition, the dependence of these predators on pilchard and anchovy is probably greater than previously speculated. This dependence on prey species has further implications regarding the management of all three species. Several cases of over fishing and subsequent stock-collapse of pelagic species have occurred in the last century, for example, the collapse of pilchard stocks off South Africa in the 1960's. These collapses can have serious ramifications for the predators of the species concerned (Duffy *et al.*, 1985). In Chile, the anchoveta (*Engraulis ringens*) collapsed in 1973, leading to the subsequent collapse of the Chilean snoek four years later. While the prey population recovered within 15 years, snoek numbers remained very low (Cury *et al.*, 2000). As snoek, pilchard and anchovy are all commercially important and intimately ecologically linked species, their utilisation and its effects must be continually monitored.

2. Although snoek are regarded as generalist predators, the act of migration for the sake of feeding by females seems to imply some form of prey selection towards clupeoids on their part. Pilchard and anchovy almost completely dominate the diet of the fish in winter and spring (more so than in summer and autumn) in this region (Chapter 3). This could mean that there might be some active selection by female snoek to meet their energy needs during spawning. Between these two main prey types, there appears to be a preference for anchovy over pilchard (Chapter 3). Snoek are presently seen as generalist feeders, and further study on the topic of selectivity may cast a new light on their feeding strategy.

3. As mentioned, pilchard and anchovy undergo shifts in dominance in the Benguela ecosystem (Shannon *et al.*, 1992). This means that the predominant species in the system

could determine, or influence, the spawning and migration behaviour of snoek. The diet results in Chapter 3 indicate that anchovy are available to snoek exclusively in the inshore regions along the coast, as their range does not usually extend to the offshore regions sampled (Crawford, 1989; Roel *et al.*, 1994). It could be reasoned that if anchovy were dominant, constant inshore feeding migrations on the West Coast would be necessary for female snoek. Pilchard are available in both the inshore and offshore diets (Figure 3.3), as their range extends further offshore, meaning that they are potentially available to snoek on their spawning grounds. In Region 4, for example, pilchard are found offshore in the spawning area, and the sex ratio is not skewed in this area (Griffiths, 2002). The implication is that when pilchard are dominant, female snoek may not have to migrate inshore as frequently in order to feed, as the food source would be at hand. This is particularly true in light of a pattern noted by Barange *et al.* (1999) over the 1990's, where pilchard consistently occurred further offshore in times when anchovy numbers were low. This would mean that sex ratios would potentially be more even during snoek spawning in pilchard regimes, and less so in anchovy regimes. In addition, increased pilchard availability on snoek spawning grounds could possibly mean increased spawning success for snoek, as the added costs of inshore migration would be reduced.

4. Due to the skewed sex ratios during spawning, there are probably considerable differences between the diets of male and female snoek on the West Coast, during this time (Chapter 3). Unfortunately, inadequate sample sizes precluded the accurate testing of this theory in this study (Chapter 2), however, distribution patterns and regional diet differences on the West Coast would seem to confirm this. Outside spawning times, the diets of the two sexes are probably more similar as both sexes are found inshore, and the generalist feeding strategy is probably more applicable, although females seem to retain a slight dominance inshore throughout the year (Appendix 4.3).

5. In light of the uneven sex ratios, differential fishing effort by the trawl and hand-line fisheries, could have potential effects on the stock structure of snoek. The trawl fishery operates

offshore, during the spawning time of snoek, and accounts for about 60% of the total catch. The other 40% is made by commercial and recreational handline-fishers, close inshore and mainly during autumn and summer (Griffiths, 2002). Heavier exploitation by the trawl fishery during the spawning period, could result in an artificially skewed sex ratio, as female numbers in the trawled areas are lower than males (± 2:1), due to inshore migrations (Appendix 4.4). It could be predicted that the trawl fishery catches more males during spawning, and thus the possibility and effects of an uneven sex ratio across the whole stock should be considered in future research.

CONCLUSIONS

Snoek feeding intensity alters throughout the year, in relation to spawning and the preparation for spawning. This probably implies some form of behavioural alteration in the foraging activity of the species from season to season. As physiological rhythms and the period of preparation for spawning are theoretically driven in part by available food, year to year variation in prey abundance may conceivably affect the timing and duration of the spawning period of snoek, as well as the spawning success of the fish. The 'ramper' pattern in snoek probably evolved as a function of seasonal prey availability, as Crawford and de Villiers (1985) state that the biomass of prey available to snoek declines in summer, the non-spawning period.

The seasonal differences in feeding intensity also point toward applications for future sampling. As the greatest percentage of fish feed in winter and spring, these would seem the ideal times to conduct a diet survey. The probability of obtaining fish with stomachs containing food is higher at this time, and thus fewer samples would be needed overall. Differences in feeding intensity also imply that if a calculation of annual consumption were attempted, seasonally weighted consumption indices would have to be used (Palomares and Pauly, 1989). This would involve calculating the exact differences in seasonal feeding intensity and deriving a consumption constant for each season, in order to standardise the estimates. In addition, it is worth considering that seasonal differences in consumption probably occur in many species

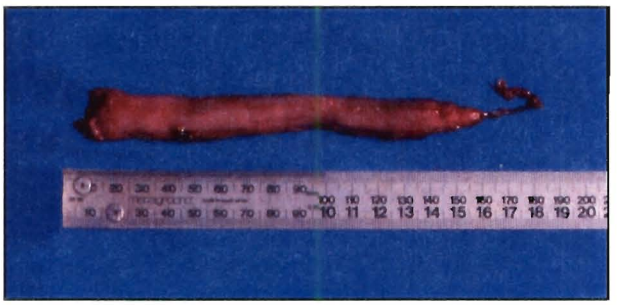
within this ecosystem, which could determine patterns of aggregation and dispersal (Link and Burnett, 2001) (e.g. snoek consume more during spawning, and move inshore on the West Coast to feed). These fluctuations, if built into existing models, could improve their accuracy and predictive power.

The cost of spawning is most likely higher for females of this species than for males. Females compensate for this cost by migrating inshore (on the West coast) to feed on high-energy clupeoids, which are in constant supply here (Chapter 3), probably resulting in differences in the diets of the two sexes on the West Coast, during the spawning period. Due to the differences in the distribution ranges of the two main prey species, and the fact that they undergo shifts in dominance in the system, female migration behaviour may alter depending on whether pilchard or anchovy is dominant. This is a theory that has yet to be tested, but if true, it may have implications regarding snoek distribution, and thus the fishery and the management of the species. Differential fishing effort by the trawl and handline fisheries also requires consideration, as higher fishing effort by the trawl fishery, could result in permanently skewed sex ratios, due to the relative availability of each sex to the trawlers during spawning.

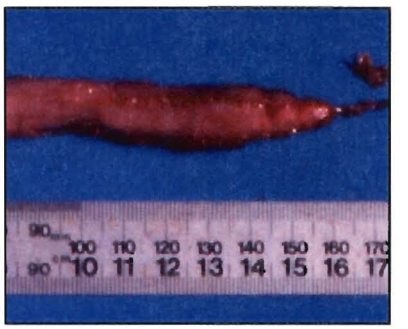
APPENDIX 4.1: Photographs of snoek stomachs, showing fat classes 0 – 4, as defined by the visual index scale ('Methods' section).

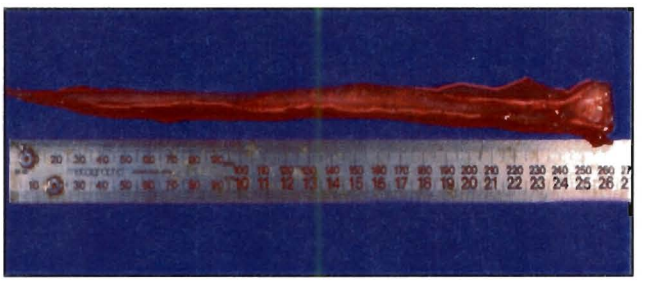
WHOLE STOMACH

DETAIL

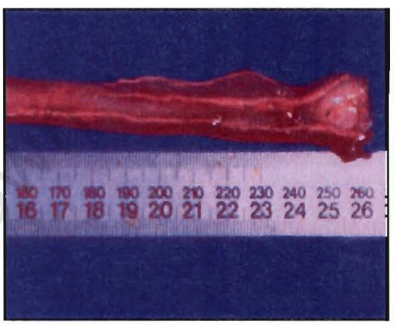


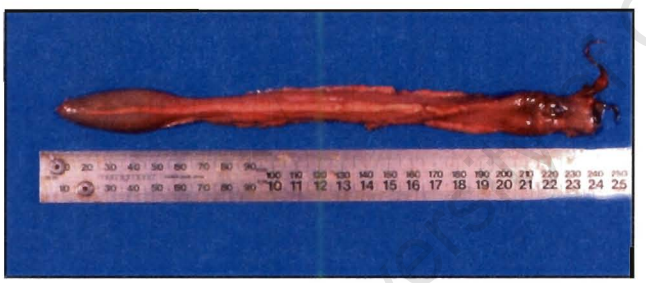
Fat class 0



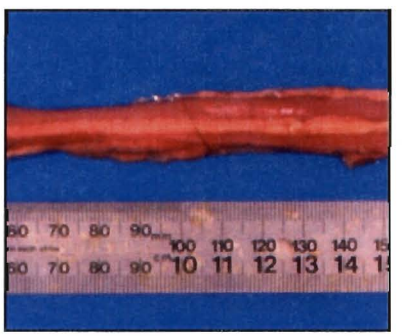


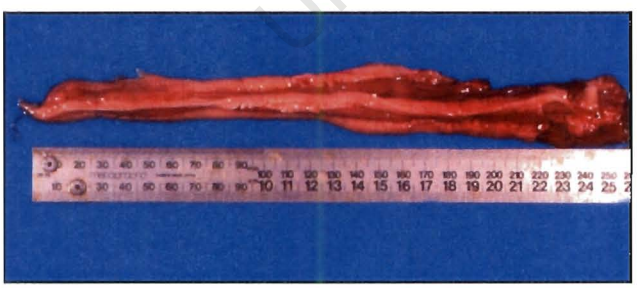
Fat class 1



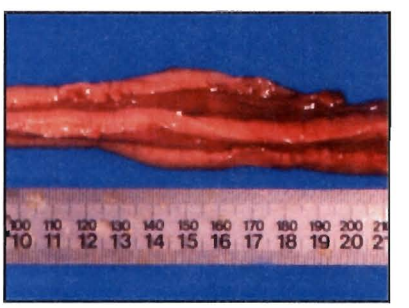


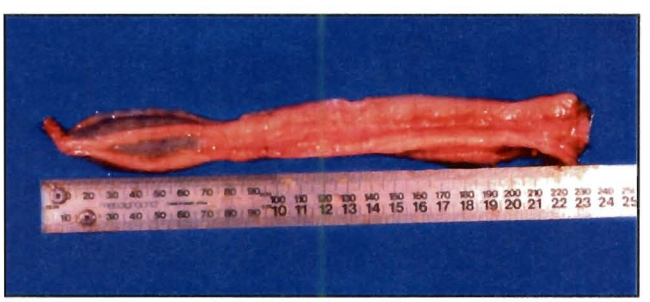
Fat class 2



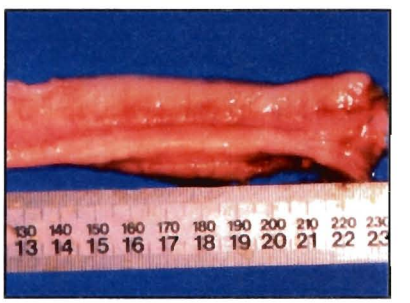


Fat class 3

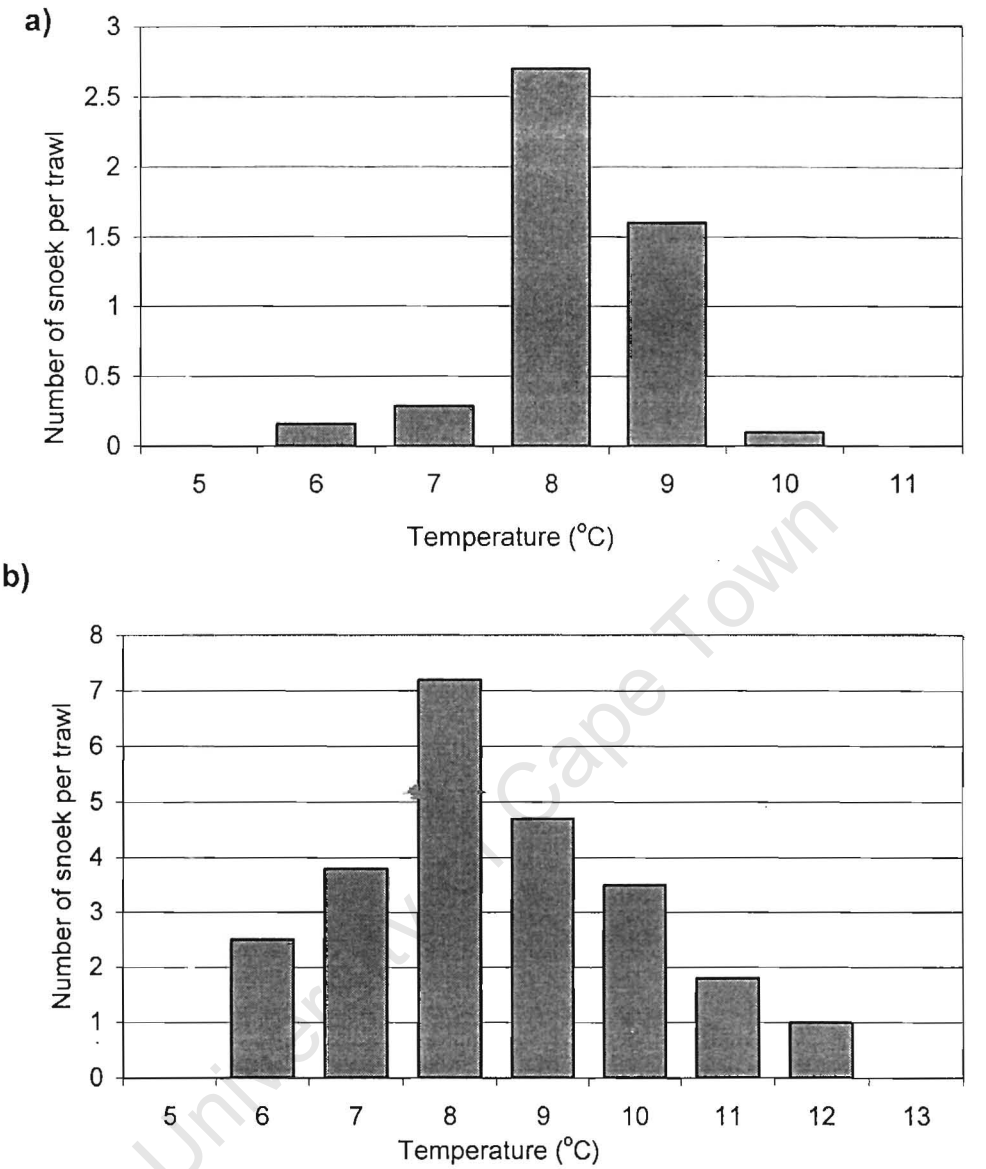




Fat class 4



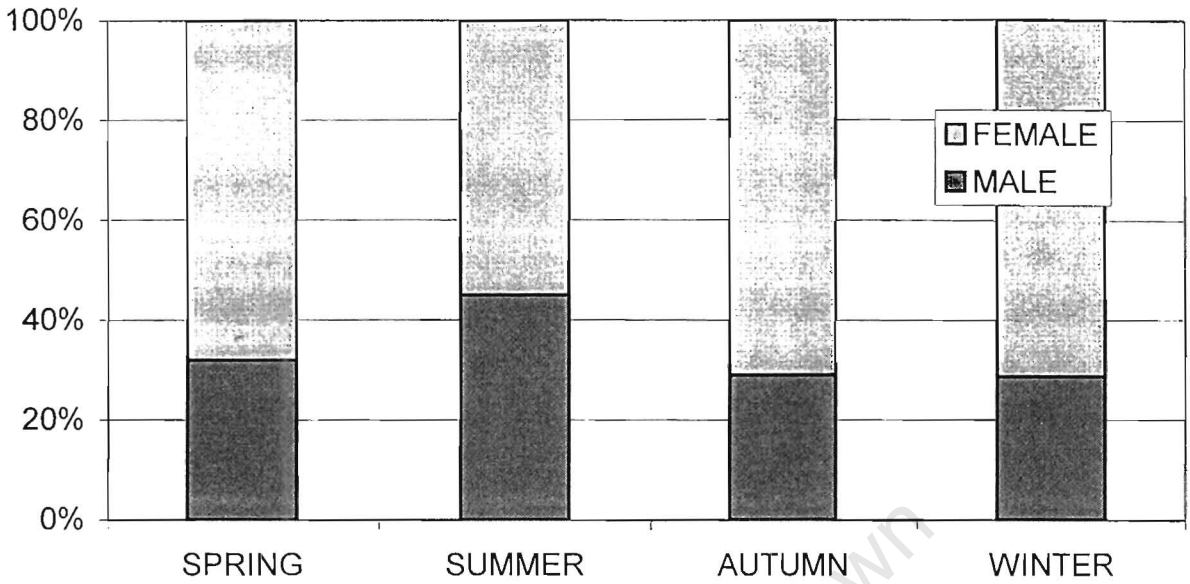
APPENDIX 4.2: The relationship between snoek abundance and bottom temperature on the trawl grounds (unpublished data, Marine and Coastal Management). Sample sizes – no. trawls: summer n = 861, winter n = 348; no. snoek: summer n = 1415, winter n = 1646.



Bottom temperature and number of snoek caught per trawl in a) summer, and b) winter. Data supplied by MCM •

• Demersal (trawl) databases of Marine and Coastal Management (MCM), Private BagX2, Roggebaai, Cape Town, South Africa, Unpublished Data.

APPENDIX 4.3: Comparative sex ratios of adult snoek on the spawning grounds and in inshore waters



Mean sex ratio of males to females for region 3, inshore, over all years combined. Griffiths (2002), found significant deviations from unity in this area, and surmised that the females, being serial spawners, move inshore to feed between spawning bouts.

APPENDIX 4.4

The sex ratios of adult fish inshore and offshore (reproduced with permission from Griffiths, 2002)

INSHORE		**OFFSHORE**	
SUMMER / AUTUMN	WINTER / SPRING	SUMMER / AUTUMN	WINTER / SPRING
	Regions 0 – 3		
M : F	M : F	M : F	M : F
1 : 1.8	1 : 2.9	1 : 1.2	2 : 1
	Regions 4 – 5		
M : F	M : F	M : F	M : F
1 : 2	1 : 1.2	-	1 : 1.6

Chapter 5:

Daily and weekly variation in the diet and diel feeding periodicity of snoek (*Thyrsites atun*)

Chapter 5

INTRODUCTION

The majority of fish feeding studies are conducted over extended time-periods, in order to encompass seasonal, annual or intra-annual variations in diet. Sampling in such studies may be undertaken infrequently, with long gaps between samples. The gathering of data over short time intervals, however, can provide information on predator feeding and prey species, which is overlooked by more sporadic sampling. Not only can these data show the variation in the diet and behaviour of a fish over short time periods, but they may also give some idea of the movement patterns and availability of prey species at localised scales. A species that has high levels of short-term dietary variation would logically require a higher sampling frequency to achieve an accurate annual diet description, and thus the scale of diet variation is an important determinant of sample design. The aim of this chapter is to demonstrate the advantages and uses of data gathered at frequent intervals and over short time periods, as well as to describe the patterns of diet and predation at this temporal scale for snoek (*Thyrsites atun*).

Diel patterns

Variation

Fish species differ widely in their daily feeding activities (Mathur, 1973). Some species feed discontinuously, according to recurrent cyclic diurnal rhythms, while others feed continuously throughout the 24-hour period, with intermittent peaks in intensity (Jenkins and Green, 1977). Knowledge of when and how often fish feed in the wild is useful when estimating parameters such as daily ration and consumption rate (Elliot and Persson, 1978; Pennington, 1985). These parameters (e.g. gut evacuation rate, consumption rate, daily ration, and annual consumption) are vital to the understanding and quantification of energy conversion efficiency and fish feeding ecology. They are also fundamental in the construction of ecosystem models such as ECOPATH and ECOSIM, which attempt to quantify the energetic flows between various components of the trophic webs in a system (Hobson, 1978; Palomares and Pauly, 1989). Such

models have both theoretical benefits and practical applications, particularly in fisheries management (Pauly, 1989).

In nature, it is difficult to quantify diel feeding patterns in fish as feeding trends must be observed continuously over many 24-hour periods (Jenkins and Green, 1977). This is necessary, because feeding patterns in most species are a function of many interacting factors and constraints, both external (environmental), and internal (physiological) (Godin, 1981). Abiotic factors influencing the timing and intensity of feeding behaviour include light intensity (Keast and Welsh, 1968; Jenkins and Green, 1977; Godin, 1981), season, spawning behaviour, prey distribution, size and abundance, water temperature and the presence of other predators, which may present a danger or compete for the same resource (Jenkins and Green, 1977; Harris *et al.*, 1988). Physiological factors affecting feeding behaviour centre on the 'motivational urge' of the fish to feed. They include the fullness of the gut (in turn, depending on when the fish last ate, and how much it consumed), as well as its gut evacuation rate (Godin, 1981). In addition, the animal's nutritional needs may change according to its physiological state, e.g. the build-up of reserves for spawning (Chapter 4) (Shul'man, 1974, Link and Burnett, 2001).

When studying diel patterns, it is also important to take into account individual variation in the feeding behaviour within a population (Eggers, 1977, Keast and Welsh, 1968). This is especially so with opportunistic or generalist feeders, where all encounters with prey will be optimised by the predators, and feeding may thus follow a random pattern (Wooton, 1990; Gerking, 1994). These factors need to be recognised and studied if a true understanding of the feeding periodicity and behaviour of a fish is to be gained (Kogan, 1970)

Data collection and uses

Diel patterns of feeding are studied in the field by examining the stomach contents of fish, in particular the ratio of gut weight to fish weight (Swenson and Smith, 1972; Elliot and Persson, 1978; Harris *et al.*, 1988). Large differences in the mean gut fullness over time are indicators of feeding periodicity (Jenkins and Green, 1977). These differences are not always an accurate

measure, however, particularly in fish with very slow evacuation rates. In such species, feeding cycles may exist, but cannot be detected because there is always food present in the stomachs (Harris *et al.*, 1988). A further source of error in this measurement technique is post-collection digestion, especially if the fish are not killed immediately after they are caught. This often occurs in trawled samples, where digestion continues as fish are retained by trawling gear, leading to incorrect estimations of feeding times (Eggers, 1977). Such errors can be corrected through actual observations of feeding behaviour, or by mathematically correcting for retention times (Swenson and Smith, 1972; Jenkins and Green, 1977).

It must be stressed that stomach content mass can only provide information on the food consumed and the feeding habits of the fish (Pauly, 1989). Additional information, specifically digestion or evacuation rate, is required to calculate consumption estimates which can be incorporated into trophic models (Swenson and Smith, 1972; Pennington, 1985). Only the most rudimentary estimates of evacuation rate can be obtained from field data, and then only when the fish have a pronounced and fixed cyclic feeding patterns (Jenkins and Green, 1977, Eggers, 1977). This is done by calculating the change in stomach content mass over time after a bout of feeding, producing an (usually) exponential evacuation rate equation (Eggers, 1977). In reality, this is often not possible, and evacuation rate must be calculated in other ways.

There are two methods commonly employed for this. Either direct calculation, by means of laboratory studies, or indirect calculation, using bioenergetic models (Wooton, 1990). The former technique is by far the most common, and involves estimating digestion rate by feeding captive fish and periodically sacrificing the animals to weigh their gut contents. This method rests on the assumption that the laboratory conditions accurately reflect field conditions, and that the stress of handling has no effect on the evacuation rate of the sample animals (Swenson and Smith, 1972). Bioenergetic modelling involves calculating the evacuation rate of a fish based on its growth rate, energy and nitrogen requirements and food conversion efficiency (Wooton, 1990; Elliot and Persson, 1978). This method requires a lot of information on the growth and energy budgets of the fish and relationship between these and food conversion

efficiency, which is not always available (Elliot and Persson, 1978). Once feeding chronology and evacuation rate are known, consumption rate can be calculated.

As consumption rate often varies from season to season (Chapter 4) in relation to periods of gonad development (Link and Burnett, 2001), annual consumption is often calculated by using seasonally weighted estimates of daily ration (Palomares and Pauly, 1989; Bogstad *et al.*, 1995). Annual consumption can then be used in providing quantified estimates of the trophic dynamics of the predator-prey relationships in the ecosystem.

Diel variation in diet

In many cases, it is not only feeding intensity that varies diurnally, but also diet (Keast and Welsh, 1968). This variation can be regular and predictable e.g. when the prey organisms are only available at certain times of the day as a result of set movement patterns such as vertical migration (Keast and Welsh, 1968). In other cases, diel diet variation is irregular, and is simply a result of random prey movements and availability (Keast and Welsh, 1968; Curio, 1976; Harris *et al.*, 1988). Prey movements and thus availability to predators are often a result of the availability of their own food resources. Thus, knowledge of the feeding ecology and behaviour of prey species can aid in the prediction of knock-on effects when it comes to predator feeding patterns.

Week-to week variation and sampling frequency

Intra–haul correlation

Since many marine organisms occur in clustered distributions such as schools (e.g. pelagic fish) or swarms (e.g. mantis shrimps), prey distribution is often patchy and unpredictable. Prey patches are a result of the social behaviour of the species and also relate to environmental conditions, which are variable in time and space. This variation in prey distribution means that the stomach contents of predators will also inevitably be highly variable in time and space. The fish caught and compared at one sampling station are more likely to have greater similarities in their diets than fish caught at several different stations. This similarity is known as intra-haul

correlation, and is discussed in detail by Bogstad *et al.* (1995). Tirasin and Jørgensen (1999) note that intra-haul correlation is a very important source of variation in the prey composition of stomach contents. Samples of schooling fish such as snoek, whether trawled or line-caught, represent a highly clustered arrangement. Precision and accuracy in diet description depend not only on sample size, but also on the number of locations and times sampled (Green, 1979;Bogstad *et al.*, 1995; Tirasin and Jørgensen, 1999).

Naturally, the purpose of the study is of importance here. The implication is that if the aim was, for example, to study the diet of a species over one season, sampling would have to take place throughout the season, at varying times during the day, and over a wide geographical range. Although this factor would seem self-evident, it is often overlooked or marginalized. Bogstad *et al.* (1995) stress that sampling fish is essentially a non-random procedure due to the grouping behaviour of both predator and prey. They propose that a degree of randomness must be introduced artificially in order to get a better overall picture of the diet of the species concerned. By mathematical examination of variance and intra-haul correlation, they calculated that by collecting fewer stomachs and sampling more stations, they were able to reduce the degree of variance and maximise their precision in diet description.

Sampling fish diet too frequently in one area over too short a period introduces bias into diet estimates. However, in order to accurately quantify diet over a period of time (e.g. a year or a season), sampling cannot be too infrequent either. As Hynes (1950) and Hyslop (1980) point out, all seasons, times of day, water depths and the whole distribution range of a species should be sampled in order to gain a clear picture of its diet and feeding behaviour. In Chapter 2, the importance of adequate sample sizes for point diet measurement was discussed. It is proposed here that, to describe diet over (for example) a season, the number of samples taken over that period should also be sufficient to ensure accuracy. In addition, to avoid intra-haul correlation, samples should not be 'clumped together' over short periods during the season, but should be evenly spaced in time (Bogstad *et al.*, 1995). In order to determine how regularly to sample, knowledge of the time scale at which prey availability in an area and thus dietary variation

occurs, is also necessary. Thus the design of a diet study would probably necessitate some preliminary sampling and a good understanding of movement patterns of prey, and the time-scale of their distribution changes.

AIMS

The aims of this chapter were to investigate some of the short-term trends in the diet of snoek (*Thyrsites atun*) at localised scales in the Southern Benguela Upwelling region. By examining three time-scales (diel, daily and weekly), it was hoped to gain an understanding of the scale of variation in prey distributions and thus determine a suitable sampling frequency. An additional aim of daily sampling was to determine the feeding periodicity of this species, as well as possible links between diet and aggregation behaviour or movement patterns of snoek.

Diel patterns

Trawled snoek on the spawning ground, gathered over two periods of continuous sampling (42 hrs and 80 hrs) at fixed locations, were used to investigate diel and daily trends in diet and feeding. The difference in feeding intensity between male and female fish was examined, to see if trends were consistent with those discovered in Chapter 4. If so, it was expected that females would have a higher feeding intensity than males, particularly during spawning. The position of snoek in the water column (as measured by the diel availability to the bottom trawl) was also investigated with respect to feeding.

Weekly patterns

The aim of sampling snoek stomachs on a weekly basis was to investigate the variation in diet and thus prey availability at this time scale. It was hoped that this would give an indication as to the sampling frequency required to describe seasonal diet. If the diet did not vary significantly from one week to the next, it could be argued that sampling need not be as frequent in order to maintain accuracy. On the other hand, if week-to-week variation were extensive, more regular

sampling would be required to correctly describe relative prey proportions over the season. This part of the study was thus initiated as a preliminary investigation into sampling frequency.

As snoek is such an important predator in the Benguela Upwelling System, an accurate estimate of its annual consumption would be very important in modelling the system. Both snoek and the pelagic prey it consumes are important commercially (Griffiths, 2002), and a quantitative analysis of the relevant trophic relationships would be valuable in the management of the resources in the ecosystem. It is hoped that this chapter will serve to highlight what further study is needed to estimate gut evacuation rate, and thus annual consumption for modelling purposes. In addition, the study of sampling frequency will improve sampling accuracy in future snoek dietary studies.

Week-to-week variation

A six-week sampling programme was undertaken in False Bay in autumn 2001, with the aim of collecting 100 full snoek stomachs per week. Success in obtaining this tally was dependent on the availability of snoek in the sampling area, as well as the proportion of fish in the samples with stomachs containing food. The data were collected by handline fishing, using bait or lures, usually within about 25km of the coast, at depths ranging from 10 - 30 m. Samples were obtained one day per week, and were collected either by i) linefishing by research staff, or ii) collection of stomachs from vendors of commercially caught snoek. Only five of the samples were deemed large enough to give an accurate description of the diet, and data from the third week of sampling was thus ignored. Stomachs were removed from the fish and frozen immediately in order to prevent post-mortem digestion

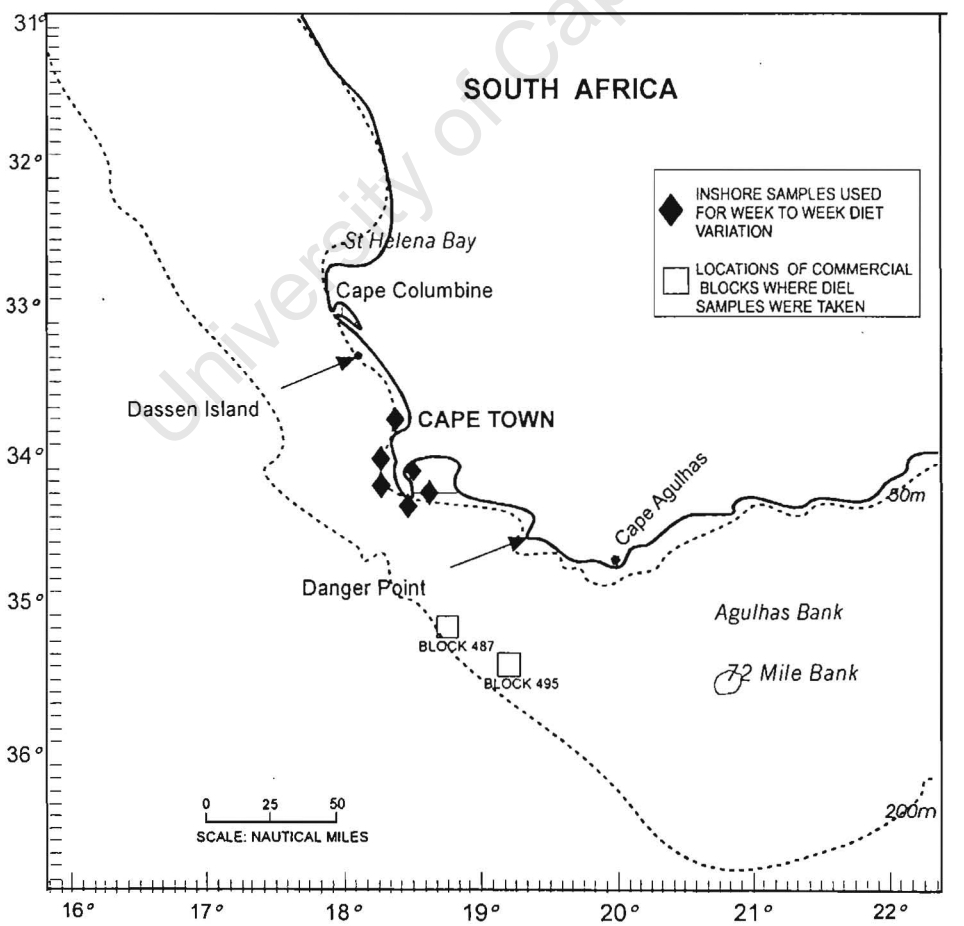


Figure 5.1: Sampling locations used in estimates of short-term diet variation in snoek.

Limited biological data were recorded, namely fish sex and fork length (to the nearest mm). Samples were thawed in the laboratory and stomach contents analysed wet, the assumption being the moisture content was the same as in a fresh sample.

Table 5.1: Macroscopic gonad stages as used a guide in field research for snoek. (Reproduced with permission from Griffiths, 2002).

Stage	Gonad appearance	
	Female	Male
1: Immature/resting	Ovaries are clear, pinkish or translucent Orange tubes. No eggs visible.	Testes clear and thread-like to pinkish-white and ribbon like.
2: Active	Slight increase in diameter of ovary. Eggs discernible to naked eye, do not occupy all available space.	Testes wider, triangular in cross-section and beige-cream in colour. Sperm present if gonad is cut and squeezed.
3: Ripe	Ovaries larger in diameter, completely opaque, and orange/yellow in colour. Eggs occupy all available space.	Testes larger in cross-section, softer in texture. Considerable quantities of sperm give them a creamier colour.
4: Ripe-running	Ovaries considerably larger in diameter, amber in colour, with a substantial proportion of hydrated eggs.	Sperm freely extruded when pressure is applied to the abdomen of the whole fish.
5: Spent	Ovaries similar in size to Stage 1. A few yoked oocytes remain which are generally aspherical and appear to be undergoing resorption.	Testes shrivelled and mottled beige and cream in colour. Small amounts of viscous semen may still ooze from the genital pore when pressure is applied to the abdomen.

Analysis

Prey items were identified to the lowest possible taxon and weighed wet to the nearest 0.1 g. Bait (in line-caught stomachs) and net-consumed items (in trawled stomachs) were generally easy to recognise and were discarded. The mass values for each prey type were summed and expressed as a percentage of the total prey mass. Unidentified prey were grouped discreetly and combined with those prey items contributing less than 5% to the diet to form the group "other".

Diel patterns

For each sample the diet was plotted in a stacked bar chart (Figures 5.2 and 5.3), over the two time-periods studied. As in Chapter 3, small sample sizes precluded the separation of data into male and female diet samples. Superimposed on the diet plots were line graphs, showing the mass (in kg) per hour, of snoek caught in each trawl. The sample sizes used are shown in Table 5.2.

Table 5.2: Sample sizes (stomachs containing food) used in the diel feeding study for snoek – no snoek were caught in the night-time trawls, so these are not indicated on the figure. The circled figures indicate samples of questionable size for accurate diet representation (based on the results of Chapter 2)

Sample 1	Day 1	Day 2			Day 3	
Time	17h10	08h20	11h20	17h20	07h20	11h20
No. stomachs	87	40	36	57	26	9

Sample 2	Day 1		Day 2			Day 4	
Time	10h30	17h20	07h30	11h30	17h30	10h00	17h20
No. stomachs	42	97	70	19	22	293	353

Stomach fullness (stomach wet mass as a percentage of fish wet mass, excluding zero values) was plotted for male and female fish separately, as per equation 4.1 in Chapter 4. The percentage of fish with stomachs containing food was also plotted for male and female fish. The data for stomach fullness were tested and found to be non-parametric, and data-transformation failed to convert samples to normal probability distributions. The significance of differences in stomach fullness between male and female fish were thus calculated statistically using a non-parametric paired test, the Mann-Whitney *U*-test (Fowler *et al.*, 1998). Statistical differences between the percentages of fish feeding for males and females were tested using Chi squared tests.

Although feeding intensity and proportions of fish feeding did vary over the time-periods studied, no clear cyclical pattern of variation appeared to exist, so the changes were not tested for statistical significance.

Week-to-week variation

The diet for each week was plotted, as was the mean diet over the six-week period. Prey proportions were subject to multivariate analysis using PRIMER® for Windows™ (release 5.0). To detect similarities between weekly diets and the overall diet, a one-way ANOSIM was performed on the data. Graphic representations of the similarity between samples were produced by means of Bray-Curtis similarity matrices, from which multidimensional-scaling (MDS) plots and cluster analyses were drawn. Two main prey types were subsequently selected (anchovy, *Engraulis encrasicolus*, and mantis shrimps, *Pterygosquilla armata capensis*) and the differences in their proportions from week to week were plotted. The difference for these two prey types from their mean value over the six weeks was also plotted.

RESULTS

Diel patterns

Diet and catch rate

In Area 1 (block 495), the diet was dominated on Days 1 and 2 by pilchard (*Sardinops sagax*) and round herring (*Eutremeus whiteheadi*), in varying proportions (Figure 5.2). Also present were hake (*Merluccius spp.*) and horse mackerel (*Trachurus trachurus capensis*). On the morning of the Day 3, round herring dominated, to be replaced at midday by hake. At this point (midday), the catch rate declined, and despite continued trawling in the afternoon, no snoek were caught, indicating that they had probably moved out of the area.

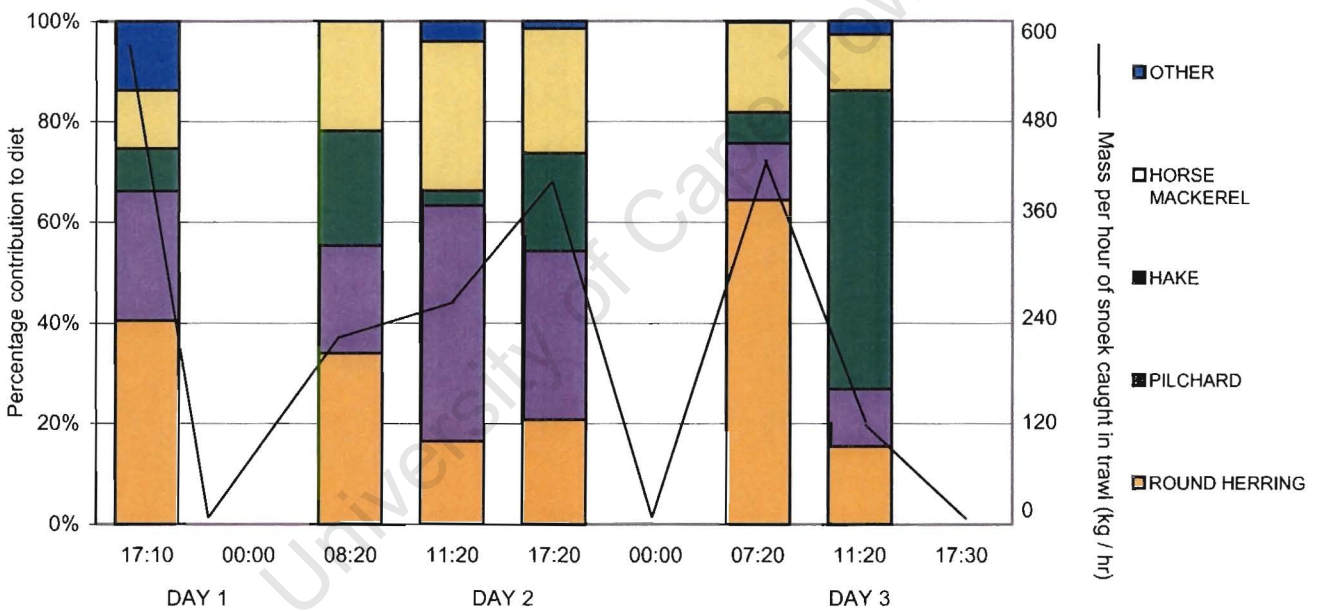


Figure 5.2: The diet and mass of snoek caught at each station in Area 1 (block 495)

In Area 2 (block 487), the diet was dominated by pilchard until midday of Day 2 (Figure 5.3). Also present in the diet were round herring, hake, horse mackerel and anchovy (*Engraulis encrasicolus*). In the afternoon of Day 2, the diet was dominated by hake, and as in Area 1, the catch declined at this point. Subsequently, sampling was done at another location, and diet was not monitored for 24 hours. The catch on the morning of Day 4 was lost due to a hole in the net, but the catches of snoek at midday and in the afternoon of this day exceeded all other catches made on the research cruise. The diet in the late morning of Day 4 was dominated by horse

mackerel, with small amounts of anchovy, round herring, pilchard and hake. In the afternoon, the dominant prey type was pilchard, with three times the proportion present in the morning. At this time, the percentages of round herring and hake had increased and the percentages of anchovy and horse mackerel had decreased.

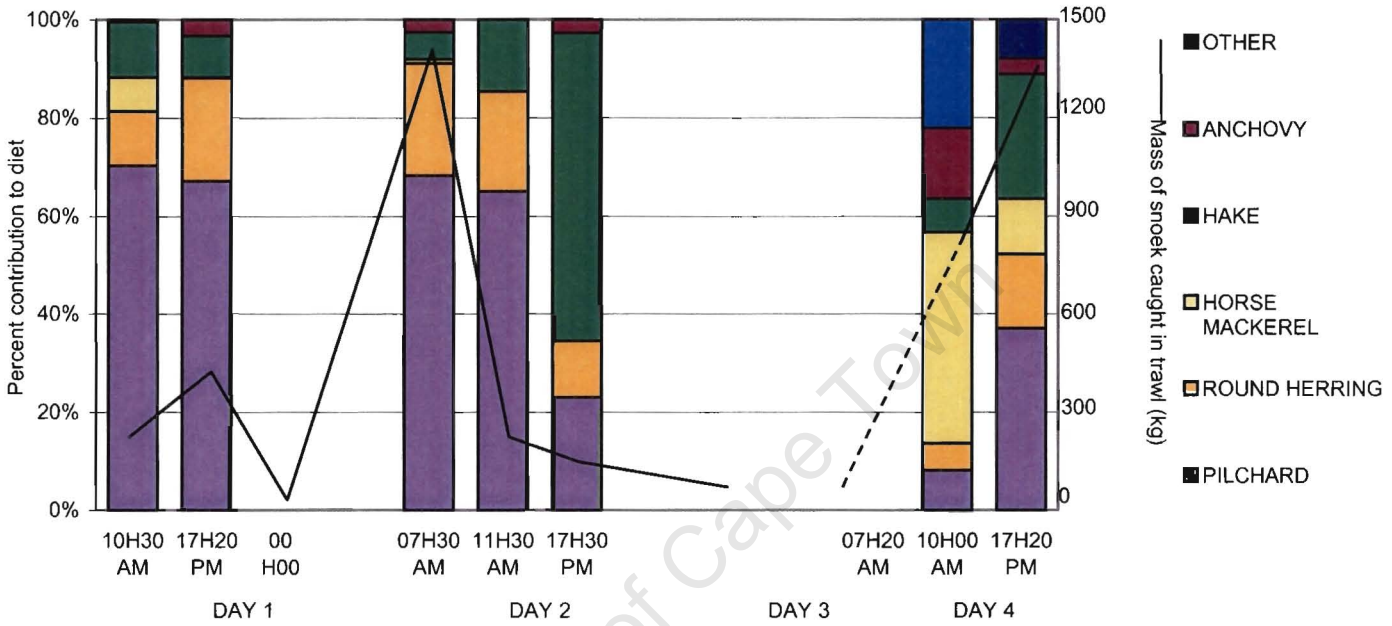


Figure 5.3: The diet and mass of snoek caught at each station in Area 2 (block 487)

The high similarity in diet in the first four trawls of each area, demonstrates a pattern consistent with intra-haul correlation.

Feeding intensity

The proportion of fish feeding and the feeding intensity of snoek do show some variation at a diel scale, particularly in females (Figures 5.4 and 5.5), although there does not seem to be any fixed daily feeding pattern. The fact that stomach fullness never dropped below 1% of body mass, and the percentage feeding dropped never below 15%, indicates that the population probably fed continuously over the 42-hour period. The consumption indices in the morning trawls which were always greater than zero, as well as the freshness of prey items (pers. obs.)

would possibly reflect feeding that had taken place during the night. Despite frequent midnight trawls throughout the research cruise, no snoek were caught on the seabed at night. Non-availability on the bottom at night, and stomach fullness indices in the morning trawls, suggest that snoek were feeding in the upper water column at night and following the vertical migrations of their prey.

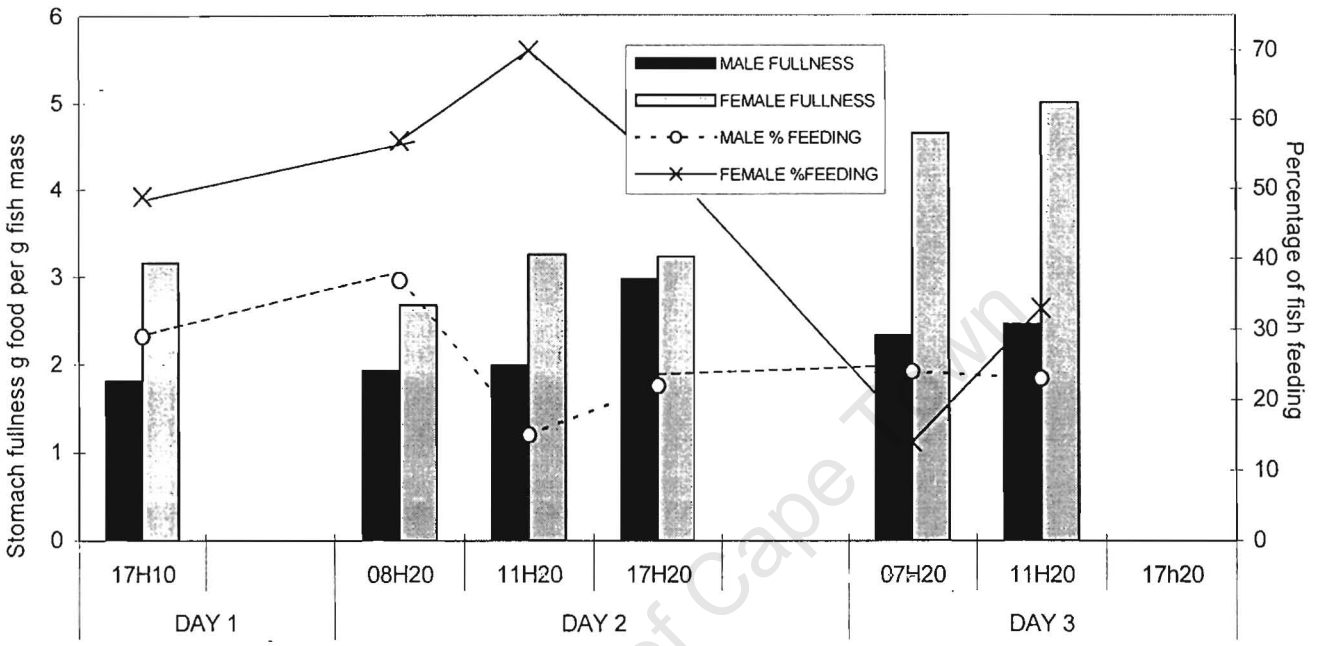


Figure 5.4: The percentage of fish with stomachs containing food (lines) and the mean stomach fullness per station (bars), for male and female fish in Area 1 (block 495).

It was found that 99.8% of all female Stage 4 fish (Table 5.1) had empty stomachs. From this it is evident that females stop feeding as their eggs begin to hydrate. The increase in ovary size is such that other internal organs are compressed, including the stomach, meaning that food cannot be ingested (Griffiths pers. comm.*). Those females feeding were of gonad Stages 2 and 3 and Stage 4 females were thus excluded from analysis. All males examined were Stage 4. A Mann-Whitney *U* - test found that females had significantly higher stomach fullness than males (Area 1: $U = 1$; $p < 0.05$; Area 2: $U = 5.5$; $p < 0.05$, Mann-Whitney *U* - test). Chi squared tests found that a significantly higher proportion of females were feeding than males (Area 1: $p = 0.043$; Area 2: $p < 0.001$).

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On Days 1 and 2, in Area 1, the percentage of fish feeding was highest in females, peaking at 70% at midday on Day 2 and dropping to its lowest level (15%) on the morning of Day 3 (Figure 5.4). This indicates that feeding in snoek probably also occurs during the daylight hours, and in the lower water strata, as trawls took place on the bottom (roughly 240 m) and prey items were fresh in many cases. Evidence from echo sounders also indicates that many of the prey species (e.g. pilchard and anchovy) are found on or near the ocean bed during daylight hours and migrate to the surface at night (although anchovy show stronger vertical migration patterns than pilchard) (Holton, 1969; Crawford, 1989; Van der Lingen, 1999). In males, the percentage feeding did not vary as much as in females, but a peak (35%) on the morning of Day 2 would reflect that more intensive feeding had possibly taken place during the first night. Feeding percent in males then dropped on midday of Day 2, and stabilised to around 20% of fish with stomachs containing food after this. Stomach fullness (in females) followed a similar trend to percentage of fish feeding, with one major discrepancy. This occurred on the morning of Day 3, where stomach fullness peaked, but the percentage feeding was at its lowest. This could mean that only a few fish in the population had actually succeeded in finding food when the sample was taken. Male stomach fullness, as with percentage feeding, was fairly constant over the time period, with a slight peak on the evening of Day 2.

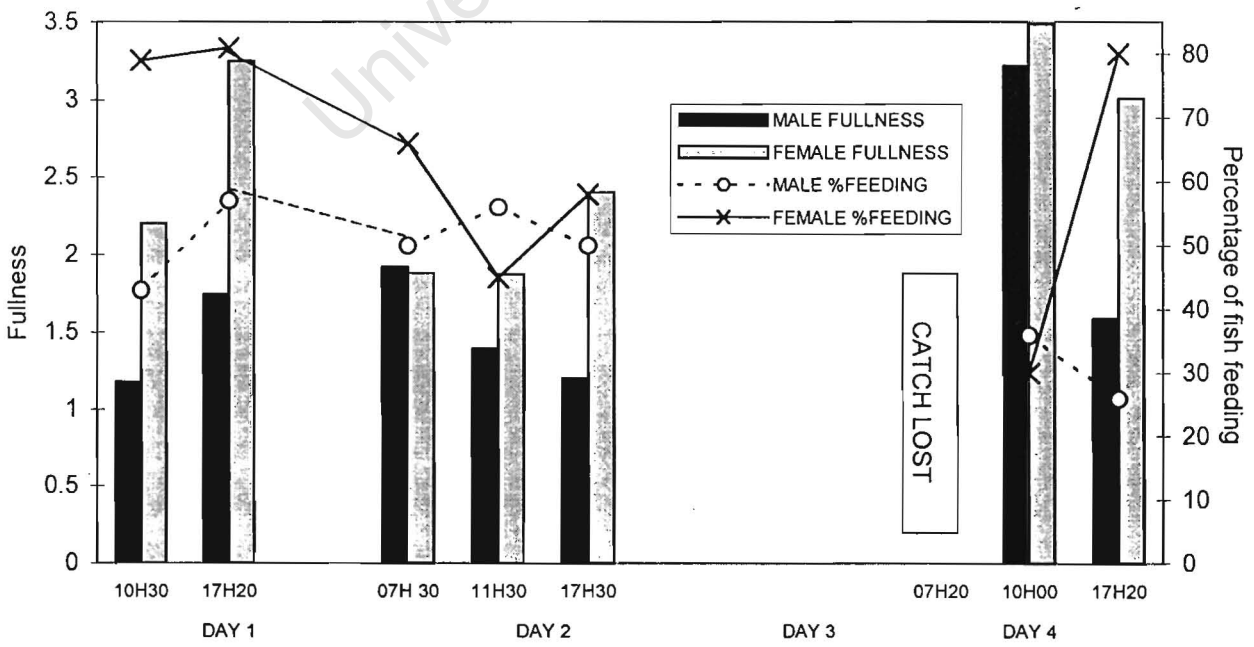

Figure 5.5: The percentage of fish with stomachs containing food (lines) and mean stomach fullness per station (bars), for male and female fish in Area 2 (block 487).

In Area 2, the trends in fullness and percentage of fish feeding (Figure 5.5) followed each other more closely than in Area 1. The peak percentage feeding for both male (55%) and female (82%) fish, as well as peak stomach fullness occurred on the evening of Day 1. Stomach fullness and fresh prey items the following morning indicated that feeding had probably continued during the night. In females, feeding declined in intensity after this, during the day (45% feeding), but rose again that evening (60% feeding). The difference in male feeding intensity between midday and evening is marginal. On Day 4, peak fullness was seen in the late morning, in those fish feeding (about 30%). The percentage feeding, however, (in females), rose to nearly 80% that evening, possibly indicating that more prey had become available during the day.

Week-to-week variation

The stacked bar chart (Figure 5.6) clearly shows that the diet of snoek varied greatly over the six-week period. The diet in Week 1 was dominated by horse mackerel (*Trachurus trachurus capensis*), which appeared infrequently in the other weeks. Week 2 was dominated by anchovy (*Engraulis encrasicolus*), which also dominated Weeks 5 and 6. Pilchard (*Sardinops sagax*) was the second-most prevalent prey in the diet in Week 2, and this was the only time that it appeared in any substantial quantity in the diet. Week 3 was completely dominated by mantis shrimps (*Pterygosquilla armata capensis*). Mantis shrimps were present in the weeks subsequent to this sample, but in declining quantities (Weeks 5 and 6). The diets in Weeks 5 and 6 were similar, with more round herring (*Eutremeus whiteheadi*) occurring in Week 6 than in any other week. The sixth column on this figure represents the mean diet over the six-week period. This mean appears most alike to Week 5, but is not closely mirrored by the diet in any one of the weeks over the sampling period, but rather appears an amalgamation of five diverse diet samples.

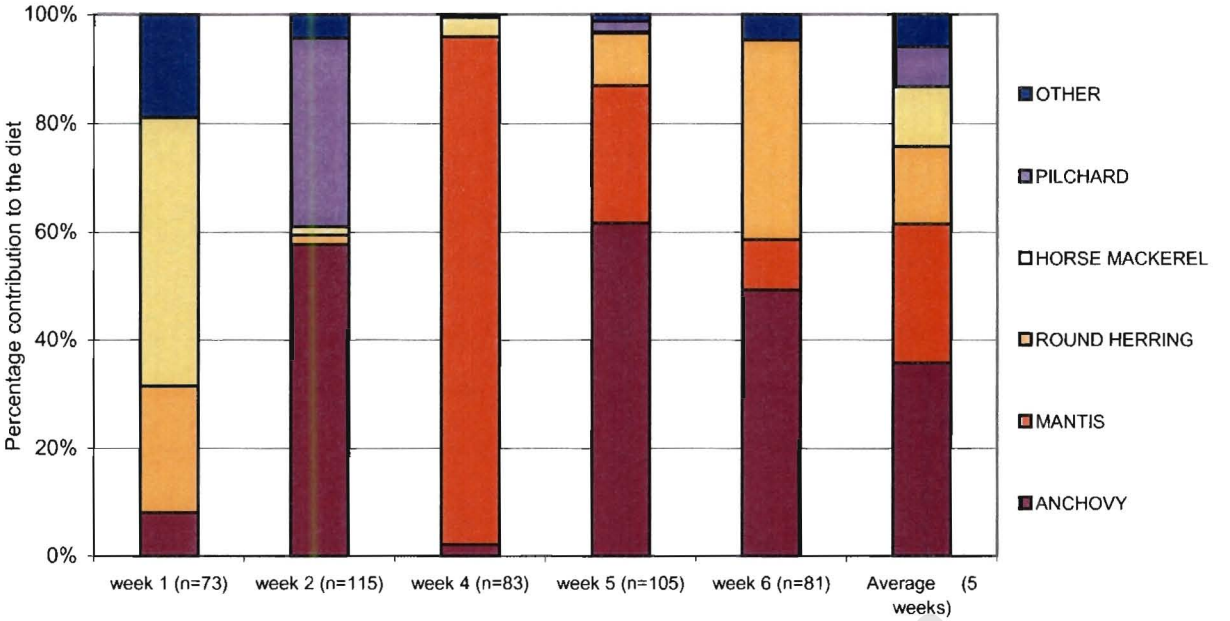

Figure 5.6: Short term (week to week) variation in snoek diet, as compared with the mean diet over the six-week period.

Figures 5.7 a) and b) give an indication of the high degree of variation (showing the absolute differences in prey proportions) in the diet of snoek over a short time period, or within a season in a fixed area. The largest difference in prey types from week to week predictably occurs after the two-week gap (Week 2 – Week 4), as there was a break in the continuity of sampling (Figure 5.7 a)). The smallest difference was between weeks 5 and 6, where the prey proportions were similar.

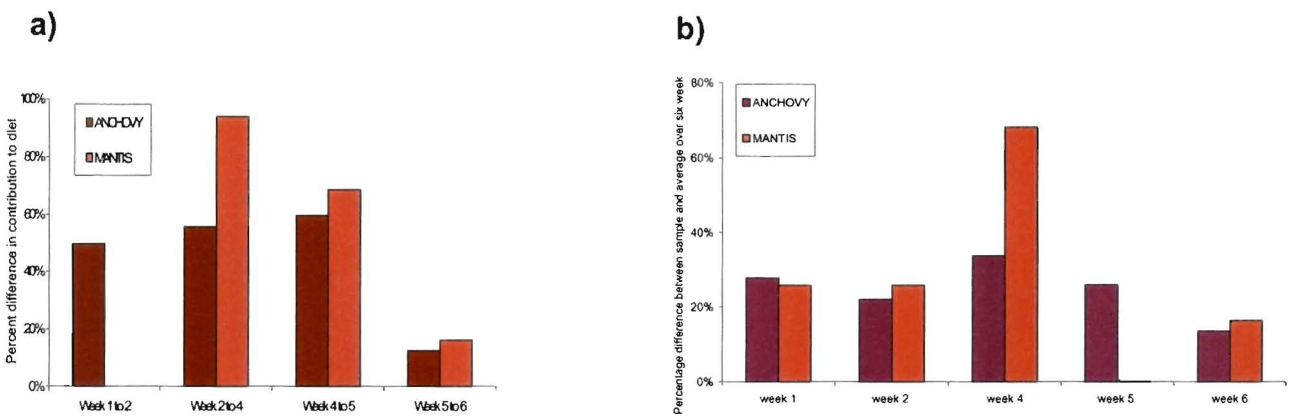

Figure 5.7: Percentage difference (absolute) for the two main prey types a) from week to week for the six-week period, and b) between each sample and the mean diet over the six-week period.

The absolute difference between the proportions of the two main prey types per week and their mean proportions over six weeks (Figure 5.7b)) indicates the largest difference occurred in week 4, where the diet was dominated by mantis shrimps.

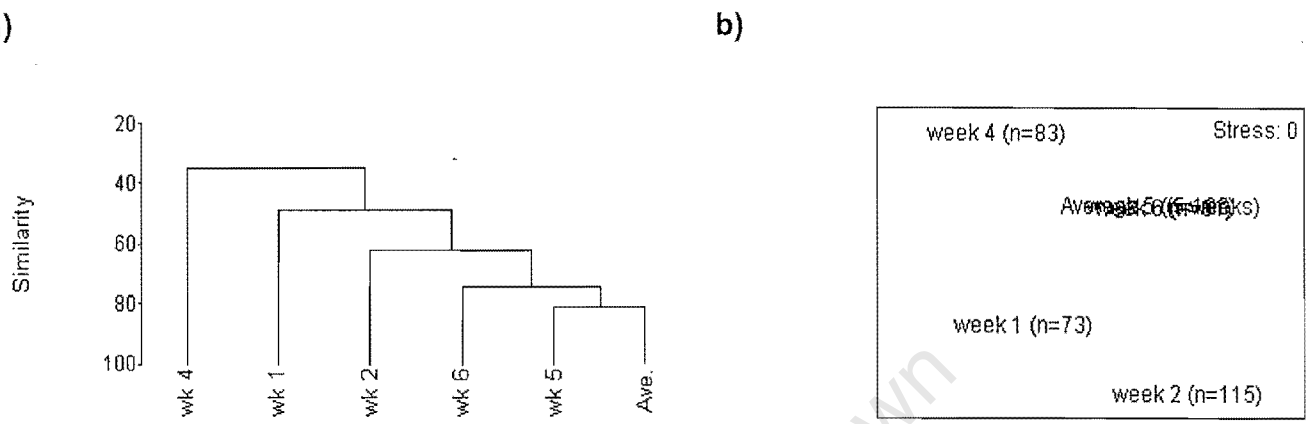

Figure 5.8: a) Cluster analysis and b) an MDS plot of the similarity of diet samples over the six-week sampling period, based on the Bray-Curtis index.

Figures 5.8 a) and b) are graphic representations of the similarity between the samples. Weeks 5 and 6 have the highest similarity (approximately 70-80%) to the overall diet for the period as seen in the MDS plot, which is also reflected in the cluster analysis. Apart from weeks 5 and 6, there does not seem to be any similarity concerning the time series of the samples, i.e. similarity does not diminish with increasing time between samples. The stress value of zero on the MDS plot indicates that it is a good representation of the data (Clarke and Warwick, 1994). A one-way ANOSIM indicated no significant degree of similarity between any of the samples, or the samples and the mean ($R = -0.68$; $p = 0$).

DISCUSSION

Diel patterns

Diet and catch rate

An interesting relationship between diet and catch rates was evident in both areas sampled. On Days 1 and 2 of sampling, snoek ate mostly pilchard and round herring (Area 1) and pilchard (Area 2). On the Day 3 (Area 1) and late on Day 2 (Area 2), the main prey item became hake, presumably due to a change in availability of the various prey types. In both cases the point at which the diets changed, coincided with much lower catch rates. In Area 1, snoek subsequently became unavailable to the trawl. As sampling was conducted elsewhere after the poor catches were made in Area 2, this pattern could not be conclusively followed here. As discussed in Chapters 3 and 4, it is evident that clupeoids are the chief source of energy for spawning snoek, particularly females, who migrate inshore, in order to feed on them. In this case, it is postulated that the fish switched to feeding on hake when no clupeoids were available, in order to satiate their need for food but, judging from their availability in Area 1 (Day 3) and lower catch rate in Area 2 (Day 2), they may have eventually moved on to follow their preferred food resource. This trend could suggest that, although snoek are opportunistic and flexible in their feeding choices, they have certain preferred prey types (e.g. a positive selectivity for anchovy, Chapter 3). On Day 4, clupeoids were available in Area 2, possibly in larger numbers (as seen by the proportions of prey in the diet), and the numbers of snoek caught increased substantially from previous levels. As feeding intensity is highest in winter and spring, when the snoek are spawning (Chapter 4), their feeding motivation would probably also be highest at this time. This is evidenced by the fact that although their preferred diet of clupeoids was replaced by hake for a period, feeding intensity itself did not decrease.

Feeding intensity

In a 1979 study, Nepgen (1979a) proposed that snoek feed in the early morning, and to a lesser extent in the late evening. This theory was based on anecdotal information gained from fishermen, as the best handline catches are generally made at these times. Indeed, interviews with fishermen during this study yielded the same comments (n = 15). Nepgen (1979) also

stated that snoek feed until their stomachs are full and then cease feeding until they are completely empty again. Based on the species found in the stomachs, he also comments that the majority of feeding takes place on the surface, and that only occasionally is food taken on the ocean floor, or in deeper water (Nepgen, 1979a). Dudley (1987) concluded that snoek fed continuously throughout the day with a peak in the afternoon, although his sampling was non-continuous and his sample sizes very small. The aim of 24-hour sampling was to investigate the periodicity of snoek feeding, and to determine whether they did show either of the previously mentioned patterns.

It was evident from the study of diel feeding intensity that snoek do not exhibit any fixed, recurrent feeding cycle during their spawning period. Rather, feeding seems more-or-less continuous throughout the day and night, with certain irregular peaks and dips in intensity.

The population as a whole did not exhibit any integrated cyclic feeding pattern, which would indicate that feeding rhythm was largely an independent matter in the case of each individual fish, and that the non-periodic feeding pattern observed was a result of variation from fish to fish. In other words, each individual would probably have a certain feeding periodicity, but not the snoek population as a whole. It was stressed in Chapter 3 that snoek are generalist predators and will opportunistically feed on whatever food is available to them (with a few preferred species). Feeding periodicity in generalist predators does not often follow strict diurnal rhythms and foraging times tend to be flexible, in order to take advantage of whatever prey is available at the time (Mathur, 1973; Curio, 1976). It is noticeable that the food type available did not seem to affect feeding intensity, but may have influenced the distribution of the predators.

The data, and therefore scope of this study were very limited, and in order to quantify diel feeding accurately in this species, further study would be required. As Jenkins and Green (1977) state, it is not possible to conclude diel patterns by sampling only a few 24-hour periods, and that long-term experimental analysis is required. The results obtained here could have been influenced by several factors other than feeding patterns, and more intensive study could

quantify or account for factors which may cause variation in the diel cycle, such as individual variation, environmental factors, and so forth. It is also possible that no feeding periodicity exists in snoek at this particular time of the year. Swenson and Smith (1972) state that feeding cycles can be regular at certain times of year, and irregular at others, meaning that studies would have to be conducted in different seasons. It is possible that snoek feeding during spawning are more aggressive and feed continuously, as the drive to feed is much stronger, because of the fishes' need to maintain reserves for reproduction (Chapter 4). This would mean that consumption rates would be higher, and intervals between feeding would be shorter, resulting in the appearance of continuous feeding (Eggers, 1977). There is possibly a more pronounced diel feeding pattern, as suggested by Nepgen (1979) and the fishermen interviewed, in non-spawning fish. Their observations were based on line-caught snoek that occurred close to the shore, which were probably not spawning and thus possibly had a lower hunger drive, as fish with a 'ramper' feeding strategy return to 'normal' feeding in non-spawning periods (Chapter 4; Link and Burnett, 2001).

Vertical migration and use of senses

Throughout the sampling trip, no snoek were caught on the bottom by the trawl at night, a pattern also noted by Nepgen (1979). This movement of the snoek off the ocean floor at night was the one recurrent diurnal pattern observed in this study. This movement may be attributed to the migration of many of their prey species (e.g. clupeoids and lanternfish, Chapter 3) into the upper layers of the ocean between sunset and sunrise, as indicated by acoustic surveys (Holton, 1969; Hobson, 1978; Prosch, *et al.*, 1989; Van der Lingen, 1999). This migration of the deep scattering layer (DSL) is brought about by the concomitant migration of food resources utilised by the prey species, namely plankton, to the surface at night (Holton, 1969; Crawford, 1989). Peak feeding in these prey species is thought to be around dawn and dusk, but their feeding and movements can be very variable, leading to knock-down variations in their predators' feeding patterns (Hobson, 1978). Hake, another of the prey species of snoek and a predator of clupeoids, are also known to move up off the bottom and into midwater at night (Payne *et al.*, 1987). In the same way that snoek may follow their preferred prey species from

one region to another, they also seem to follow the vertical migration in order to maximise the amount of time they are potentially in contact with prey species.

Feeding intensity, the freshness of prey items in the stomachs, and the evidence of clupeoid distributions from acoustic surveys, indicates that feeding probably also takes place on the bottom during the day, in some cases more so than on the surface at night, although unfortunately it was not possible to get actual measurements of feeding intensity at night. It is thought that this similarity between night and daytime feeding is possible for predators in this system, as pilchard shoals retain their shoal-density day and night in the Southern Benguela. Maintained shoal integrity is not the case with small pelagics in some other systems (Van der Lingen, 1999).

It has been established that snoek probably feed in deep water (150 – 450 m) on the spawning grounds, offshore) during the day, and that very little light penetrates below around 70 m (Hobson, 1978). At night, feeding takes place on the surface, where very limited amounts of light exist. Predatory fish that hunt under such conditions are thus forced to rely on exceptional vision, or senses other than vision, to detect their prey (Hobson, 1978; Gerking, 1994). Non-visual senses are enabled by chemical receptors, either olfactory or gustatory, and are adapted to following the odour-trails of prey animals (Hobson, 1978; Gerking, 1994). Snoek have very large eyes, possibly adapted to hunting in near-complete darkness. It is also possible that snoek rely on non-visual senses to augment their vision, in order to follow prey in conditions where sight is impaired or impossible.

Sexual differences

The trend of higher feeding intensity in females served to confirm the patterns observed in Chapter 4. Females feed more intensively and consume more than males, possibly due to higher costs of reproduction. Feeding intensity in females was also more variable than in males, which could be attributable to food availability. The higher feeding intensity of females may indicate that they have higher motivational levels to feed, and may thus be more competitive,

aggressive and flexible in their feeding strategy. It is possible that this pattern was exaggerated by the fact that the sexes were separated for sampling purposes. Females were separated and sampled before males on the research cruise, meaning that males would have undergone a longer period of post-catch digestion. However, the pattern was still observed when this practice was not employed (Chapter 4).

Week to week variation

In the 24-hour study, the diet of snoek did not vary noticeably from one day to the next, until sudden changes occurred. From the length of diet stability, it would seem that the diet may only change significantly in an area every two or three days, depending on region and relative prey abundance. When it did change, it would probably not change for very long, as the snoek seemed to follow their preferred prey source. Although not mathematically tested, these trawled samples would have shown a high degree of intra-haul correlation, as they were done at such short intervals. Thus, while they were appropriate for describing diel trends, they could not have been used in a longer-term study, without additional sampling (Bogstad *et al.*, 1995).

The inshore variation in prey proportions between the samples taken weekly was high. Proportions varied from week to week, and for the most part, showed little similarity to the mean for the six-week period. This lack of similarity in diet is a powerful demonstration of the importance of sampling frequency in the accuracy of diet description. It also shows the high degree to which prey resources and distributions vary in the area sampled. The Southern Benguela is described as highly variable and patchy (Smale, 1992), and prey species undergo wide-ranging migrations throughout the system (Chapter 3), resulting in an ever-changing degree of availability to predators. Thus, in order to quantify accurately the proportions of prey consumed, it is necessary to sample regularly, over wide areas of the predators' distribution (Hynes, 1950; Hyslop, 1980). In the case of snoek, sampling at least once per week should suffice for future seasonal or annual diet descriptions. A more detailed study on diel diet variation and the temporal scale of prey fluctuations is required, as well as an assessment of the

spatial scales of diet variation, so that comprehensive and inclusive sampling programmes can be designed.

CONCLUSIONS

It can be concluded from the data available in this study, that snoek feed continuously throughout the day, and do not appear to have any fixed feeding times. It must be added, however, that further study is needed on this topic, encompassing longer periods, more frequent sampling, and taking into account the various factors that affect feeding periodicity. As no fixed feeding pattern could be established, no attempt was made to estimate evacuation or consumption rates and daily ration in snoek, for modelling purposes. To this end, only two options remain. Firstly, a tank study on captive snoek could be undertaken in order to study evacuation rate. This option would likely prove very difficult, as it is not only costly, but snoek do not acclimate well to laboratory conditions, and tend to die shortly after capture (Griffiths, pers. comm.). Another option would be the calculation of consumption using the model developed by Pauly (1989), based on the physiology and aspect ratio of a species (Chapter 1).

From the change in distribution of snoek with the prey species availability it would seem that snoek have a definite preference for clupeoid-type prey, and will actively follow these prey, both on their vertical migrations, and from region to region. Knowledge of the movements of snoek in relation to its preferred prey could be useful in predicting snoek movements at an immediate scale, e.g. sampling or fishing. The week-to-week variation in diet is a simple indicator of the scale at which variation occurs in this system, and demonstrates the need for frequent sampling. It is concluded that in order to describe diet over a time-period such as a season, sampling should occur at least once weekly. By doing so, it would be possible to encompass the full range of dietary variation that would occur over an extended period of time. The conclusions yielded by this chapter are only preliminary indications and require more in-depth research.

Chapter 6:

Synthesis and conclusions

Chapter 6

The purpose of this research

An increasing proportion of the fisheries research conducted each year has an underlying practical purpose. Applied research is gaining momentum, as the need for sustainable resource use becomes an ever-increasing reality. Models (such as those described by Hollowed *et al.*, 2000 and Whipple *et al.*, 2000) combining aspects of economics, oceanography, meteorology, ecology, biology and other disciplines, are enhancing our ability to understand and manage complex ecosystems. The construction of these models is facilitated by data gathered through multidisciplinary research efforts, such as the Benguela Ecology Project.

The Benguela, as with all upwelling systems, is highly productive and subject to variation on many scales, be they diel, seasonal, annual or decadal. The upwelling of nutrients on the western coast of southern Africa supports a high plankton biomass, which in turn supports large populations of primary and secondary consumers. These support a range of tertiary consumers and top predators, one of which was the focus of this study. Because upwelling is dependant on oceanographic and climatic conditions, it is subject to fluctuations in frequency and intensity, which can have knockdown effects on the biota. Recruitment success (egg and larval transport) in many species is also dependant on variable wind and current patterns, and can thus vary in response to these. It would follow that having evolved in a changeable system, many of the organisms in question would have adapted to the fluctuations by having highly plastic life histories, which would serve to buffer somewhat the effects of the variation. Logically, predators in such an ecosystem experience variation on more than one level. Not only are they subjected to environmental variation, but to the fluctuations in their prey resources, which are dependant in turn on fluctuations in the biomass of lower trophic levels. Superficially, it would appear impossible to model and forecast such variation. However, once the links between environment and biota and between the different trophic levels are established through research, a degree of predictability is introduced. In other words, it becomes easier to envisage the functioning of the ecosystem by observing its component parts.

This study is regarded as part of the research process discussed. It has been previously established that snoek (*Thyrsites atun*) is an important predator of pelagic fish stocks in the Benguela Upwelling System. This means that it is an important component part of this system, and understanding its role would be vital for modelling the ecosystem.

Snoek diet has been previously studied, but the studies done were limited by small sample sizes and infrequent sampling (Chapter 1). Earlier studies (Nepgen 1979a and 1982, Crawford and de Villiers, 1985) were also based on erroneous assumptions regarding the annual migration of snoek and the seasonal availability of anchovy (*Engraulis encrasicolus*) to the predator. A more recent study by Griffiths (2002) provided vital information on the life history and diet of the species. Regarding diet, it was revealed that snoek show ontogenetic diet shifts, that differences existed between the diets of fish in inshore and offshore waters, and that female snoek periodically move inshore to feed over the spawning period. However, because it was such a wide-ranging study, many topics could not be addressed, and the purpose of the present study was to investigate some of these. They included: whether diet or feeding intensity exhibited seasonal patterns of variation; the links between diet and abundance of prey species and selectivity by snoek; diurnal and small-scale variation in diet; differences in reproductive costs between males and females, etc.

Synthesis

Sampling accuracy

The accuracy of previous work done on the diet of snoek was called into question in Chapter 1 and the importance of precision in diet studies was investigated in Chapter 2 and the second half of Chapter 5. If the diet descriptions of a species are to be used for modelling purposes, it is vital that samples of stomachs be of sufficient size to describe prey proportions accurately (Ferry and Calliet, 1996), so that confident conclusions can be drawn, and comparisons made. Diet must also be sampled throughout the distribution range of the species, and at all times of year, season and day (Hynes, 1950). This allows for an estimation of annual diet which, with

weightings for seasonal changes in diet, provides a full, balanced picture of yearly prey consumption.

As snoek diet had frequently been inadequately sampled in the past, the use of statistical tests in Chapter 2 and frequency testing in Chapter 5 were aimed at determining how much and how often to sample snoek in order to accurately describe the diet in future studies. The emphasis of testing procedures in Chapter 2 was on finding simple, easy ways to assess the robustness of diet data. It was found that the two most effective means of testing sample size sufficiency were cumulative diversity curves and cumulative percentage curves, and both are recommended for use in future diet studies. More complex tests exist than those used here, but they tend to be time-consuming and may impact on the actual time spent focused on the study. Cumulative diversity curves were considered suitable only for predicting precision in the description of the presence and absence of prey species in the diet (i.e. diet diversity), and are not adequate on their own.

- For snoek, the recommended range of sample sizes for diet diversity estimates is 55 (± 25) stomachs containing food, depending on diet diversity.
- Cumulative percentage curves, where the percentage difference in the main prey proportion decreased from one 10-stomach class to the next as sample size increased, was considered suitable for estimation of sample size for the description of exact prey proportions. For snoek, this estimate was 75 – 80 (± 25) stomachs containing food.
- Improved accuracy with increasing sample size was further demonstrated by the reduction in standard error, which reached the 5% level after a mean of 88.9 (± 12.7) stomachs containing food had been examined for the offshore samples and 85.7 (± 20.7) stomachs examined for the inshore samples.

Lastly, an equation cited by Duffy and Jackson (1986), for the calculation of optimum sample sizes was used. This equation produced some unreasonable and unattainable sample sizes (with median values of 90-100 stomachs ± 45), but it did emphasise the importance of the actual prey proportions in the diet when testing for suitable sample sizes. In specialist or selective

feeders, where one prey type is chosen over all others and the proportion of this prey type dominates the diet, there would be a greater chance of encountering this prey type in diet samples. Hence, a smaller number of samples would be needed to provide an accurate description of the diet. Also important to consider is the fact that predicted sample sizes only apply to fish with stomachs containing food, and depending on the proportion of fish feeding, much larger samples would have to be taken. Knowledge of feeding periodicity (if it exists) would thus be useful in knowing when to sample to maximise the number of stomachs containing food.

Sampling accuracy and weekly diet variation was examined in Chapter 5. Large variations existed from week to week in the diet of snoek over a small area, and no statistical similarity existed between each week or any one week and the average over the six-week period. This indicated that regular sampling would be required to describe the diet accurately over longer periods, such as a season or a year.

In conclusion, it is recommended that between 75 and 120 snoek stomachs containing food be sampled roughly once per week to gain an accurate measure of prey proportions in future studies. In order to determine actual sample size (including empty stomachs), subsampling on site would help determine the proportion of stomachs containing food.

Seasonal diet variation

It was demonstrated in Chapter 3, as well as in previous snoek diet studies, that snoek prey on a wide variety of species. In this study, they included 11 pelagic teleosts and 11 demersal teleosts, as well as eight crustacean, four cephalopod and one annelid species. The aim of this portion of the study was to discover whether any of these species showed seasonal patterns in the diet of snoek, which could be related to their own seasonal movement patterns. The two main prey species, pilchard (*Sardinops sagax*) and anchovy (*Engraulis capensis*), showed year-round abundance to snoek inshore around the Cape Peninsula, essentially refuting previous

theories and assumptions (e.g. Crawford and de Villiers, 1985). Lesser prey types showed subtle seasonal patterns in the diet: Round herring (*Etrumeus whiteheadi*) was available all year round, except during their peak spawning period (spring) when their distribution extends further offshore than the region sampled. Horse mackerel (*Trachurus trachurus capensis*), consumed as juveniles by snoek in inshore regions, were present in the diet during their peak recruitment times (autumn, winter). Mantis shrimps (*Pterygosquilla armata capensis*) were unavailable to snoek in winter, when they are thought to occur further south than the area sampled. They were most available in summer, during high upwelling periods. Hake (probably juveniles) were only present in the inshore diet in autumn and winter, corresponding to their proposed migration around the Peninsula at this time. Regional (in-offshore) differences in diet were much more marked than seasonal differences, mainly characterised by a greater percentage of hake and an absence of anchovy in the offshore diet. New findings on pilchard and anchovy as prey species were made: there was a close correlation between their relative abundance in the diet and in purse-seine catches (r=0.6), but snoek showed a positive selectivity toward anchovy.

It was concluded from the results of Chapter 3, that:

1. Although there was a correlation between the abundance of pilchard and anchovy and their relative proportions in the diet, selectivity by snoek toward anchovy means that snoek diet could not be used as a fine-scale indicator of the abundance of these two species. Rather, it could serve as an indicator of broad-scale patterns such as regime shifts.
2. The dominant clupeoid (pilchard or anchovy) in the system at any one time may determine the behaviour, movement patterns and even spawning success of snoek.
3. Female inshore feeding migrations (Chapter 4) may lead to sexual diet differences during certain times of the year.

Physiology, spawning and feeding intensity

The relationship between physiological state, feeding intensity and spawning in snoek was investigated in Chapter 4. Griffiths (2002) showed conclusively that snoek are indeterminate serial spawners, with peak spawning from late winter to early spring. It was demonstrated in the

present study that the spawning period of snoek coincides with a period of maximum feeding intensity. It was concluded from this that snoek conform to the 'ramper' feeding strategy proposed by Link and Burnett (2001). It follows from the differential feeding intensities throughout the year that weighted consumption estimates would have to be used to calculate annual consumption.

The time of spawning coincided with the lowest levels of body fat and relative condition, and the highest levels occurred in autumn, immediately prior to spawning. The decline in fat content was significantly higher in female fish than in males, despite the fact that significantly more female fish were feeding and they had significantly greater meal sizes. This suggests that the reproductive costs to females may be higher than in males, a pattern often observed in serial spawners (Shul'man, 1974).

Year-round availability of pilchard and anchovy are probably essential for spawning and recruitment success in snoek. Females are possibly compensating for higher reproductive costs by migrating inshore to feed on these species during spawning. Male fat and condition also decline during spawning, indicating that they could also benefit from more plentiful food resources by migrating inshore. In males, this movement would, however, mean less available time for spawning, as their higher spawning frequency would almost certainly be interrupted by migration. Having high quality food available year-round may mean that the overall fecundity of this snoek population is higher than those populations that rely on lower-energy food (e.g. Australian snoek, which feed mainly on euphausiids).

Differential fishing pressure and uneven sex ratios during spawning could result in a permanently skewed stock structure without careful management, given that the trawl fishery, which operates in winter on the spawning grounds, accounts for 60% of the reported annual catch. The implication is that more males would be caught at this time than females, given their dominance on the spawning grounds.

Diel variation in diet and feeding intensity

No previous research had been done on the diel diet and feeding intensity of snoek, based on continuous 24-hr monitoring, prior to this study, and the only information that existed on feeding periodicity was anecdotal evidence from fishermen, suggesting that snoek fed most often in the early morning and late afternoon, and Dudley's study, based on very small and infrequently gathered samples (Nepgen, 1979a; Dudley, 1987). In addition to diet and feeding periodicity, the relationship between feeding and the position of snoek in the water column was investigated within the diel time frame

It was found that snoek did not exhibit any structured diel feeding rhythm, but rather that they fed continuously over the 24-hr period, with slight peaks in intensity. Because this study was conducted on the trawl grounds during spawning, it is thought that the feeding drive of the snoek sampled might have been stronger than at other times of the year. According to the 'ramper' feeding pattern, feeding returns to normal levels during non-spawning periods. This means that with a lower hunger-drive, feeding may have a more fixed diel pattern in non-spawning times, a change which has been observed in other species (Link and Burnett, 2001).

Snoek were not caught on the bottom at night. From this fact, as well as documented movements of their prey species, the stomach fullness values and the relative freshness of prey items, it was concluded that snoek on the trawl grounds were feeding on or near the sea bottom (150-250 m) during the day, and on the surface at night, following the vertical migration of their prey. Because they were feeding on the bottom in conditions of near-complete darkness, it was speculated that non-visual senses may be used to augment vision under certain conditions. There was limited evidence that the availability of snoek to the trawl in an area may have been positively related to the proportion of clupeoid prey available to the predator, as catches declined when hake began to dominate the diet. With the limited data available, no estimates of actual consumption rate or daily ration could be obtained for modelling purposes.

Future research

As with most research, for each question answered, others will inevitably arise. Each of the subjects examined in this study presented avenues for future research, which will now be discussed:

In order to accurately model the trophodynamic relationships of snoek, it would be essential to continue sampling the diet, possibly over a wider area of the species' distribution range, as the area covered by this study was fairly limited. Continued sampling would mean that comparisons could be made, both between different regions along the coastline and over extended time periods. Data on snoek diet has been collected, albeit sporadically, for at least 40 years, and further data collection would allow decadal scale comparisons to be made, in lieu of factors such as regime shifts, or El Ninõ events. Possible differences in diet between male and female snoek exist during spawning periods on the West coast, due to female migration. An attempt could be made to quantify these differences, and thus produce weighted estimates, to give a comprehensive picture of annual relative prey proportions in the diet. This would, however, require information on relative abundances of prey in the diet over large spatial scales. Selectivity toward anchovy by snoek was an interesting pattern, which was previously undocumented. The analysis of selectivity was very limited in this study, and the subject warrants further examination regarding selectivity towards other species in the diet. It may also elucidate aspects of snoek aggregation, movement and migration.

It was found in Chapter 4 that the feeding intensity of snoek is not constant throughout the year. This means that the exact differences in feeding intensity from season to season must be calculated and used to create formulae, which will serve to standardise seasonal consumption estimates that will facilitate accurate annual consumption estimates. Calculation of the consumption per relative prey proportion, as well as feeding intensity in juveniles and sub-adults would further increase the accuracy of estimates in this regard. In tandem with a stock assessment and data on population structure, very sound estimates of total consumption by the population could be made for the purposes of modelling. It was proposed in Chapter 4 that the

constant year-round availability of high-energy clupeoids to snoek might mean that its overall fecundity is higher than populations that feed on lower-energy resources. Although fecundity is very difficult to test, a comparison may give an indication of the plasticity of snoek life history and the relationship between spawning and available food resources. The predicted effects of differential fishing effort on the sex ratio of this species should be carefully examined in order to assess any potential long term changes in population structure and potential fecundity of the population, caused by possible higher catches of male fish on the trawl-grounds during spawning periods (due to female migration). This could be achieved by monitoring the sex ratios in both trawl and line catches on the West Coast, and calculating total catch per sex for the species.

As diel feeding periodicity was only tested in winter, during spawning, it cannot be conclusively said that fixed diel feeding patterns do not exist at other times of the year. Because snoek exhibits the 'ramper' feeding pattern, feeding intensity was at a maximum during the study period and would have returned to normal during non-spawning times, meaning that the continuous feeding observed may not be a year-round pattern. Thus, diel periodicity should be tested during non-spawning periods as well, and data are needed over many more 24 hr periods than were used in this chapter. As it was not possible to calculate daily ration or gut evacuation rate in Chapter 5, this should be a topic of focus in future research. Estimates of these parameters, as well as stock and snoek biomass assessments would be essential in order to calculate annual consumption and update the role of the species in model systems in which it has been previously included, such as ECOPATH and ECOSIM. The calculation of evacuation rate could be most effectively achieved by undertaking a captive feeding study, but because snoek do not survive well in captivity, other means may be necessary. As discussed in Chapters 1 and 5, Pauly's (1989) mathematical model, based on the aspect ratio of the caudal fin could be employed to this end. As snoek is considered one of the most important predators in the Benguela Ecosystem, its inclusion as a consumer into trophic models has already been undertaken. The fine–scale nature of this diet study could possibly provide additional data for inclusion into models, which could greatly increase understanding of the functioning of the

system. Inferences could be made on the behaviour of snoek under different regimes and conditions, and its effect on prey populations could also be assessed. In addition, the effects on the snoek population of the fisheries both for snoek and its prey species could be estimated.

Before this study was undertaken, the role of snoek as a predator was well known, but remained largely unquantified on a fine spatio-temporal scale. The results of this study have furthered the understanding of the feeding ecology of this species. The variations in feeding intensity from season to season and between sexes, the dependence of snoek on a year-round supply of clupeoids around the Peninsula, and the other aspects revealed here will hopefully make modelling and managing the species easier, or elucidate further steps needed to make this possible. The guidelines for attaining sampling accuracy will ensure that further studies and diet estimates are more accurate, and could possibly also be applied in the sampling of similar predatory species.

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